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CLASSIFICATION OF THE ORDER EOBLATTIDA (INSECTA: BLATTIDEA) WITH DESCRIPTION OF NEW TAXA

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The order Eoblattida (= Grylloblattida), assigned to the superorder Blattidea (Insecta), is revised. A total of 17 families are included in this order: the extinct Eoblattidae, Protophasmatidae, Cacurgidae, Mesorthopteridae, Ideliidae, Permotermopsidae, Euryptilonidae, Atactophlebiidae, Bardapteridae, Megakhosaridae, Blattogryllidae, Daldubidae, Idelinellidae, Permopectinidae, Soyanopteridae, and Doubraviidae and the extant Grylloblattidae. Fossil representatives of the order are known from the Paleozoic of North and South America, Eurasia and Africa and from the Mesozoic of Eurasia, Africa and Australia. Recent representatives of the order live in Canada, United States, Russia, China, North and South Korea and Japan. The family Taiophlebiidae from the Permian of Brazil is synonymized under Protophasmatidae, Permulidae and Kortshakoliidae from the Permian of Europe are synonymized under Permotermopsidae. *Heterologellus* (?) *multidiffusus* Brauckmann et Nerd, 2005 from the Carboniferous of Europe is transferred to the genus *Protophasma* (Protophasmatidae). The following new taxa of Eoblattida are described: *Lomovatka udovichenkoi* **gen. et sp. n.** (Eoblattidae; Carboniferous of Ukraine); *Pintopinna* **gen. n.** (type species *Paranarkemina martinsnetoi* Pinto, 1999, **comb. n.**; Protophasmatidae, Permian of Brazil), *Suksunus bicodex* **gen. et sp. n.** (Cacurgidae; Permian of Russia); *Taskanatus* **gen. n.** (type species *Alicula asiatica*

Storozhenko, 1997;Mesorthopteridae; Permian of Kazakhstan), *Issadophlebia fusa* **gen. et sp. n.** (Atac-tophlebiidae; Permian of Russia); *Batkentak intactus* **gen. et sp. n.** (Daldubidae; Triassic of Kyrgyzstan). *Vologdoptera maculosa* Aristov, 2009 (originally described in Kortshakoliidae) from the Permian of Russia is transferred to Orthoptera incertae sedis. The new Permian family Doubraviidae **fam. n.** is described to include *Doubravia annosa* Kukalová, 1964 (Sakmarian of the Czech Republic), *Koshelevka* **gen. n.** (type species *Cerasopterum megakhosaroides* Aristov, 2004; Kungurian of Russia); *Iva permiana* **gen. et sp. n.** and *Belebey mutilus* **gen. et sp. n.** (Kazanian of Russia). The origin of Eoblattida and its position within the infraclass Gryllones are considered; some aspects of the early evolution of Gryllones are discussed.

KEY WORDS: Insecta, Eoblattida, taxonomy, Carboniferous-Recent.

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Проведена ревизия отряда Eoblattida (=Grylloblattida), отнесенного к тараканообразным насекомым (Insecta; Blattidea). В отряд включено 17 семейств: ископаемые Eoblattidae, Protophasmatidae, Cacurgidae, Mesorthopteridae, Ideliidae, Permotermopsidae, Euryptilonidae, Atactophlebiidae, Bardapteridae, Megakhosaridae, Blattogryllidae, Daldubidae, Idelinellidae, Permopectinidae, Soyanopteridae, Doubraviidae и современные Grylloblattidae. Ископаемые представители отряда известны из палеозоя Северной и Южной Америки, Евразии, Африки и мезозоя Евразии, Африки и Австралии. Современные представители обитают в Канаде, США, России, Китае, Северной и Южной Корее и Японии. Семейство Taiophlebiidae из перми Бразилии сведено в синонимы к Protophasmatidae, а семейства Permulidae и Kortshakoliidae из перми Европы – к Permotermopsidae. *Heterologellus* (?) *multidiffusus* Brauckmann et Nerd, 2005 из карбона Европы перенесен в род *Protophasma* (Protophasmatidae). Описаны новые эоблаттиды: *Lomovatka udovichenkoi* **gen. et sp. n.** (Eoblattidae; карбон Украины); *Pintopinna* **gen. n.** (типовой вид *Paranarkemina martinsnetoi* Pinto, 1999, **comb. n.**; Protophasmatidae, пермь Бразилии), *Suksunus bicodex* **gen. et sp. n.** (Cacurgidae; пермь России), *Taskanatus* **gen. n.** (типовой вид *Alicula asiatica* Storozhenko, 1997; Mesorthopteridae, пермь Казахстана); *Issadophlebia fusa* **gen. et sp. n.** (Atactophlebiidae, пермь России) и *Batkentak intactus* **gen. et sp. n.** (Daldubidae, триас Кыргызстана). Описано новое пермское семейство Doubraviidae **fam. n.**, включающее *Doubravia annosa* Kukalova, 1964 (сакмарский ярус Чехии), *Koshelevka* **gen. n.** (типовой вид *Cerasopterum megakhosaroides* Aristov, 2004; кунгурский ярус России); *Iva permiana* **gen. et sp. n.** и *Belebey mutilus* **gen. et sp. n.** (казанский ярус России). Рассмотрено происхождение Eoblattida и его положение среди гриллоновых насекомых, обсуждаются некоторые аспекты ранней эволюции гриллоновых.

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INTRODUCTION

This study is a revision of primitive, mostly Paleozoic families of the infraclass Gyllones (divided into three superorders: Blattidea, Gryllidea, and Perlidea), treated here as constituting the order Eoblattida of the superorder Blattidea.

There is little disagreement about the compositions of and boundaries between most orders of the infractlass Gyllones in the Paleozoic. These orders include Blattida of the superorder Blattidea; Mesotitanida, Orthoptera, and Phasmatida of the superorder Gryllidea; and Perlida and Forficulida of the superorder Perlidea (Rasnitsyn & Quicke, 2002; Gorochov, 2004). The families of Gryllones not included in the above-listed orders constitute a rather large group, which has no universally accepted division into orders. These families are either combined in a single order, Protorthoptera (Carpenter, 1992; Grimaldi & Engel, 2005), or divided between several orders: Protoblattoidea, Paraplecoptera and Protoperlaria (Martynov, 1938); Protoblattodea and Paraplecoptera (Sharov, 1961); or Eoblattida and Grylloblattida (Rasnitsyn, 1980; Rasnitsyn & Quick, 2002). Some of these families are assigned to the order Protoptera (Gorochov, 2004) or the superorder Archaeorthoptera (Béthoux & Nel, 2002).

One of the purposes of this study was to revise the order Eoblattida (superorder Blattidea). The families included here in Eoblattida were assigned at different times to different orders. Handlirsch (1922) placed the families Eoblattidae and Protophasmidae in the order Protoblattoidea and Cacurgidae in "Protorthoptera vel Protoblattoida". Martynov (1938) included the families Eoblattidae and Permotermopsidae in the order Protoblattoidea; the families Ideliidae (group Idelodea), Cacurgidae (Cacurgoidea), and Mesorthopteridae (Strephocladodea) were assigned to a new order, Paraplecoptera. Sharov in *Osnovy paleontologii* (Sharov, 1962) assigned the families Eoblattidae, Protophasmatidae, and Euryptilonidae to the order Protoblattodea; the families Ideliidae (including the genus *Permotermopsis* Martynov, 1937) (superfamily Ideliidea), Cacurgidae (Cacurgidea), Mesorthopteridae (Strephocladoidea), and Megakhosaridae (Megakhosaridea) were placed by that author in the order Paraplecoptera. The family Bardapteridae was assigned in the same monograph to Palaeodictyoptera (Rohdendorf, 1962). Subsequently Sharov (1968) combined the orders Protoblattodea and Paraplecoptera into one order, Protoblattodea. The typified name Eoblattida Handlirsch, 1906 was proposed by Rohdendorf (1977) to replace Protoblattoidea Handlirsch, 1906. In *Istoricheskoe razvitie klassa nasekomykh* (1980) this order contained the families Eoblattidae, Anthracothremmidae (including Epideigmatidae and Adiphlebiidae), Anthracoptilidae, Stenoneuridae and presumably Gerapompidae (including Cheliphlebiidae); the other families of Eoblattida in the sense accepted here (Mesorthopteridae, Ideliidae, Permotermopsidae, Euryptilonidae, Megakhosaridae, Blattogryllidae, and Grylloblattidae) were assigned to Grylloblattida (Rasnitsyn, 1980). Carpenter (1992) placed all families of Eoblattida *sensu n.* in the order Protorthoptera. In *History of Insects* (Rasnitsyn & Quick, 2002) Eoblattida contained the families Eoblattidae, Protophasmatidae, and Cacurgidae (treated here as Eoblattida), Spanioderidae, Gerapompidae, and Ischnoneuridae (transferred to Cnemidolestida; Aristov, 2014), and Geraridae (transferred to Mesotitanida; Gorochov, 2004), as well as Stenoneuridae, Homalophlebiidae, Apithanidae, Coseliidae, Pachytylopseidae, Thoronysidae, Prototettigidae, and Eucaenidae (Rasnitsyn, 2002). The families Mesorthopteridae, Ideliidae, Permotermopsidae, Euryptilonidae, Megakhosaridae, Blattogryllidae, Daldubidae, Idelinellidae, and Grylloblattidae were assigned in that monograph to Grylloblattida (Storozhenko, 2002), and the type genus of Bardapteridae was treated as Insecta incertae sedis (Sinichenkova, 2002). Subsequently two other families were also included in Eoblattidae: the new family Soyanopteridae (Aristov & Rasnitsyn, 2011) and the family Idelinellidae, transferred from Grylloblattida (Aristov & Rasnitsyn, 2012).

The family Cacurgidae and the genera *Eoblatta* Handlirsch, 1906 (family Eoblattidae) and *Cacurgolopsis* Pinto et Adami-Rodrigues, 1995 (which I included in Protophasmatidae) were placed in the superorder Archaeorthoptera (Béthoux & Nel, 2002). The family Cacurgidae was placed in the order Protoptera (Gorochov, 2004). Of all above-listed fossil families of Eoblattida *sensu n.*, only Megakhosaridae and Blattogryllidae were mentioned in *Evolution of the Insects* (Grimaldi & Engel, 2005), where they were treated as stem-group grylloblattodeans.

The position of the extant family Grylloblattidae Walker, 1914 should be discussed separately. Originally this family was placed in a specially erected extant order, Grylloblattida Walker, 1914 (typified: Rohdendorf, 1977; = Notoptera Crampton, 1915; = Grylloblattaria Bruner, 1915; = Grylloblattoidea Brues et Melander, 1915). It was later shown that Grylloblattidae are related to the fossil family Blattogryllidae, and most representatives of Protoblattodea *sensu* Sharov, 1968 were transferred to Grylloblattida (Rasnitsyn, 1976). At present the relatedness of Blattogryllidae and Grylloblattidae is not doubted by most authors (Rasnitsyn, 1980; Storozhenko, 2002; Grimaldi & Engel, 2005; Huang *et al*., 2008; Cui, 2012; Wipfler *et al.,* 2014; Storozhenko & Aristov, 2014). These families share the prognathous head with "predaceous" mouthparts (Huang *et al.,* 2008; Wipfler *et al.,* 2011), midsternal suture on the pterothorax (Aristov & Rasnitsyn, 2013; Storozhenko & Aristov, 2014), large coxae approaching each other distally, and asymmetrical male genitalia (Storozhenko, 1998), as well as some less important characters (Wipfler *et al.,* 2014). According to another view, the family Grylloblattidae (order Notoptera) and the order Embioptera constitute the holophyletic taxon Idioprothoraca. This taxon is characterized by the presence of unique pseudopleurites on the prothorax, two-segmented cerci in first-instar larva, and initially homonomous wings (Kluge, 2012). According to Kluge (2012: p. 375), the fossil family Blattogryllidae does not belong to Notoptera because it has a different structure of the thorax ("prothorax is not elongated"). However, considering the above-listed combination of characters shared by Blattogryllidae and Grylloblattidae, it appears that the structure of the pleural part of the prothorax (almost never preserved in fossils) cannot be considered sufficient evidence against the relatedness of Blattogryllidae and Grylloblattidae.

Aristov (2012) and Aristov & Rasnitsyn (2013) have demonstrated the relatedness of the succession Eoblattidae–Cacurgidae–Daldubidae–Megakhosaridae–Blattogryllidae–Grylloblattidae. Indeed, the differences between these closely related families are so small that it is often impossible to draw a boundary between orders within this sequence. Cacurgidae differ from Eoblattidae mainly in SC ending on C rather than on R. Daldubidae and Megakhosaridae differ from Cacurgidae only in the more basal first bifurcation of M (Aristov, 2012). Blattogryllidae differ from Megakhosaridae only in the type of the anastomosis M+CuA, and the differences of Grylloblattidae from Blattogryllidae are mostly limited to the absence of wings in the former (Storozhenko & Aristov, 2014). Hence it is proposed to treat Eoblattidae and Grylloblattidae as representatives of the same order, which, according to the principle of priority, should be called Eoblattida Handlirsch, 1906. The following families are included here in this order: the extinct Eoblattidae Handlirsch, 1906, Protophasmatidae Brongniart, 1885, Cacurgidae Handlirsch, 1911, Mesorthopteridae Tillyard, 1916, Ideliidae M. Zalessky, 1928, Atactophlebiidae Martynov, 1930, Permotermopsidae Martynov, 1937, Euryptilonidae Martynov, 1940, Bardapteridae G. Zalessky, 1944, Megakhosaridae Sharov, 1961, Blattogryllidae Rasnitsyn, 1976, Daldubidae Storozhenko, 1996, Idelinellidae Storozhenko, 1997, Permopectinidae Aristov, 2005, and Soyanopteridae Aristov et Rasnitsyn, 2011, and the extant Grylloblattidae Walker, 1914. The most typical features for these families are the paranota of the pronotum forming a full ring which does not cover the head from above and is not pressed to the pronotum laterally and forewing with CuA which has posterior branches in the intercubital space or divides irregularly (for more details, see below).

Earlier I revised the order Cnemidolestida, in my interpretation comprising 11 families from the Paleozoic of North and South America and Eurasia and Early Mesozoic of Europe: Spanioderidae, Gerapompidae, Cymenophlebiidae, Emphylopteridae, Tillyardembiidae, Psoropteridae, Sylvabestiidae, Prygidae, Neraphidiidae, and Ctenoptilidae, previously assigned mostly to Eoblattida (Aristov, 2014).

In addition to Cnemidolestida (Aristov, 2014) and the above-listed Eoblattida, primitive Gryllones include also a rather large group of families that previously comprised the "liomopteroid complex" of the order Grylloblattida (Rasnitsyn, 1980). I assign the following families to this complex: Reculidae Handlirsh, 1906, Chauliodititidae Handlirsh, 1906, Geinitziidae Handlirsh, 1906, Lemmatophoridae Sellards, 1909, Liomopteridae Sellards, 1909, Probnidae Sellards, 1909, Protoblattinidae Meunier, 1909, Epideigmatidae Handlirsh, 1911, Camptoneuritidae Martynov, 1931, Sylvaphlebiidae Martynov, 1940, Chelopteridae Carpenter, 1950, Euremiscidae G. Zalessky, 1951, Archiprobnidae Sharov, 1961, Havlatiidae Kukalová, 1964, Skaliciidae Kukalová, 1964, Bajanzhargalanidae Storozhenko 1992, Madygenophlebiidae Storozhenko, 1992, Gorochoviidae Storozhenko, 1994, Neleidae Ansorge, 1996, Ivapteridae Aristov, 2009, and Kargalopteridae Aristov, 2009. These families are known from the Upper Carboniferous to Upper Jurassic of North and South America, Eurasia, Africa, and Australia (Storozhenko, 2002; Aristov, 2009). The following characters are especially typical of these families: the paranota of the pronotum form a ring that does not cover the head from above and has no notch on the anterior margin; in the forewing, SC joins C; M branches in the basal third of the wing, in most cases proximal to the base of RS, and in most representatives has a free base (if M_5 is present, it joins CuA proximal to its division into branches); CuA divides into CuA_1 and CuA_2 or forms a dense comb near the posterior margin of the wing; and the clavus is absent. After Grylloblattidae are placed in Eoblattida, the order name for this group which has priority over others is Reculoidea Handlirsch, 1906, proposed to include the family Reculidae (Handlirsch, 1906). It is proposed here to use for this group the typified name Reculida Handlirsch, 1906, nom. transl.; my revision of this order is currently in preparation. According to the combination of the above-listed characters, this order has to belong to the superorder Blattidea.

MATERIAL

Since continental deposits are difficult to correlate, in descriptions of the distribution of taxa I indicate regional stages. The Western European stages Namurian B and C and Westphalian A and B correspond to the Bashkirian Stage; Westphalian C and D, to Moscovian; Cantabrian and Stephanian A and B, to Kasimovian; Stephanian C and Kuzel, to Gzhelian. The North American Morrowan Stage corresponds to the lower Bashkirian; Atokan, to upper Bashkirian and lower Moscovian; Desmoinesian, to upper Moscovian; Missurian and Virgillian, to Kasimovian and Gzhelian, respectively (Davydov *et al.,* 2012). Namurian, Westphalian, Morrowan, Atokan, and Desmoinesian stages are placed here in the Upper Carboniferous (Pennsylvanian) of the Global Stratigraphic Chart. The term “Middle Carboniferous” (Bashkirian and Moscovian Stages) is used only in Russia and some other countries (Alexeev, 2006); no Eoblattida have been recorded in Russia in localities dated to these stages. Thus, all Carboniferous localities discussed below belong to the Upper Carboniferous. The North American Wolfcampian Stage corresponds to the Asselian–Artinskian stages, and Leonardian corresponds to the Kungurian Stage of the Lower Permian (Sawin *et al.,* 2008). The Kazanian Stage of Russia corresponds to the Roadian; Urzhumian, to Wordian and lower Capitanian; Severodvinian, to Capitanian; and Lower and Upper Vyatkian, to Wuchiapingian and Changhsingian Stages, respectively (Newell *et al.,* 2010).

TAXONOMY

CLASS INSECTA LINNÉ, 1758

Subclass Scarabeona Laicharting, 1781 (= Pterygota Lang, 1888)

Infraclass Gryllones Laicharting, 1781 (= Polyneoptera Martynov, 1923)

Superorder Blattidea Latreille, 1810 (= Blattopteroidea Martynov, 1938)

ORDER EOBLATTIDA HANDLIRSCH, 1906

Eoblattida: Rohdendorf, 1977: 19; Rasnitsyn, 1980: 138; Rasnitsyn, 2002: 256; Gorochov, 2004: 15; Rasnitsyn & Aristov, 2010: 17; Aristov & Rasnitsyn, 2012: 50; Aristov, 2014: 3.

Protorthoptera (part): Handlirsch, 1906: 128; Carpenter, 1992: 97.

Protoblattoidea (part): Handlirsch, 1906: 151; Carpenter, 1992: 97.

Notoptera: Crampton, 1915: 337; Wipfler *et al*., 2014: 2.

Grylloblattodea: Brues & Melander, 1915: 10; 1932: 48; Wipfler *et al*., 2014: 2.

Grylloblattaria: Bruner, 1915: 195; Wipfler *et al*., 2014: 2.

Paraplecoptera (part): Martynov, 1928: 98; Sharov, 1962: 119; Carpenter, 1992: 97.

Protoperlaria (part): Tillyard, 1928: 187; Martynov, 1938: 100; Carpenter, 1992: 97.

Protoblattodea (part): Sharov, 1962: 116; Carpenter, 1992: 97.

Grylloblattida (part): Rohdendorf, 1977: 19; Storozhenko, 2002: 278.

Type family: Eoblattidae Handlirsch, 1906.

DIAGNOSIS. Head in most cases prognathous. Pronotum with full ring of paranota, not covering head and not lowered down. Legs not modified, of medium length, hind legs somewhat longer than fore legs and midlegs, not saltatorial. Wings folding flatly, incompletely overlapping. Forewings not elytrized; precostal space or costal lobe absent. Base of RS situated in basal third of wing; M_5, if present, joining CuA proximal to its division into branches; first bifurcations of M and CuA not closely set (except in Doubraviidae). CuA not dividing into CuA_1 and CuA_2 (except in some Atactophlebiidae) or with posterior branches in intercubital space (except in some Idelinellidae). CuP simple, clavus in most cases absent (anal area not separated by deep fold and thus forming no clavus). Hindwing at rest not bent transversely, with large anal area bent underneath. Ovipositor present; cerci segmented.

DESCRIPTION. Head in most cases prognathous (except in Euryptilonidae and most Idelinellidae), with medium-sized eyes, ocelli, and moderately long antennae (except in Cacurgidae). Paranotal ring complete (except in Grylloblattidae), narrow or wide with notch on anterior margin (except in *Cucullistriga* Aristov et Rasnitsyn, 2012 and *Scutistriga* Aristov et Rasnitsyn, 2012, Idelinellidae). Legs in Cacurgidae elongated, in Idelinellidae and Soyanopteridae shortened, in other families of medium length; fore legs shorter than mid- or hind legs; hind legs longer than fore or midlegs. Apices of tibiae (except in Eoblattidae, Eutyptilonidae, Blattogryllidae, and Grylloblattidae) and tibiae themselves (except in Ideliidae) without armature; tarsus five-segmented (except in Eoblattidae and Protophasmatidae), without arolium (except in Ideliidae, Mesortopteridae and some Blattogryllidae). Basisterna of meso- and metanotum in Ideliidae, Megakhosaridae, Blattogryllidae, Idelinellidae, and Grylloblattidae with sternal suture; coxae (or their distal parts) closely set in Ideliidae, Megakhosaridae, Blattogryllidae, and Grylloblattidae (in Eoblattidae, Euryptilonidae, Idelinellidae, and Soyanopteridae, set apart). Wings folding flatly, incompletely overlapping. Precostal space and "C" (except in *Aenigmidelia* Sharov, 1961, Ideliidae) or costal lobe (except in *Permeoblatta* Rasnitsyn et Aristov, 2010, Protophasmatidae) absent. SC without swelling basally; R without posterior branches (except in some Euryptilonidae and Bardapteridae). M starting branching at some distance from M_5 (except in Daldubidae) or anastomosis M+CuA (except in Blattogryllidae), markedly distal to first bifurcation of CuA. CuA starting branching in basal third (except in some Permotermopsidae and Soyanopteridae); in some Mesortopteridae, *Cacurgulopsis* Pinto et Adami-Rodrigues, 1995, Protophasmatidae, and *Euryptilodes* Sharov, 1961, Euryptilonidae, CuA pectinate anteriad, in *Idelinella* Storozhenko, 1997, Idelinellidae, divided into CuA_1 and CuA_2. Clavus present mostly in Carboniferous forms. Venation of remigium in fore- and hindwings not homonomous (except in Blattogryllidae). Ovipositor present, in most cases long, male genitalia in most cases symmetrical (except in Blattogryllidae and Grylloblattidae). Cerci (possibly except in Idelinellidae) segmented, not modified.

COMPARISON. The order Eoblattida is especially similar to the orders Blattida and Reculida. Eoblattids are different from Blattida in paranota not covering the head from above, SC long, R and RS well differentiated, and CuA not forming regular posteriad comb of branches, approaching the posterior wing margin at an angle of about 45°, and having posterior branches in the intercubital space or branching irregularly. In Paleozoic Blattida (with some exceptions; see Discussion), paranota form a wide ring covering the head, and in the forewing SC is in most cases short, R and RS are poorly differentiated, and CuA, even if it has posterior branches in the intercubital space, forms a regular posteriad comb, which is not found in Eoblattida. Reculida are more similar to Eoblattida. The most important feature distinguishing all reculids from eoblattids is CuA without posterior branches, divided into CuA_1 and CuA_2 or branching rather distally and forming a dense comb of branches at the posterior wing margin. In Eoblattida, CuA has posterior branches or divides irregularly. Almost all Gryllones are distinguished from Eoblattida in the absence of posterior branches of CuA in the intercubital space.

Among the Scarabaeones, Ishnoneuridae and Tococladidae (suborder Strephocladina, order Hypoperlida; Rasnitsyn & Aristov, 2013) are similar to some eoblattids in forewing venation. Ishnoneuridae are distinguished from Eoblattida in CuA pectinate anteriad, without posterior branches, in most cases having fewer branches than RS. The eoblattids especially similar to Ishnoneuridae are *Cacurgulopsis* Pinto et Adami-Rodrigues, 1995 (Protophasmatidae) and *Euryptilodes* Sharov, 1961 (Euryptilonidae). The features distinguishing these eoblattids from Ishnoneuridae are limited to RS relatively small and not fused with MA, M having many branches, and the rather proximal bifurcations on the main branches of CuA, which is pectinate anteriad. A more important distinguishing feature, which makes it impossible to assign Ishnoneuridae to Eoblattida or to Gryllones in general, is the structure of the mouthparts of this family and the roof-shaped folding of the wings in some representatives. The head in Ishnoneuridae is beak-like elongate, and the mouthparts have narrow and long mandibles and maxillae. Ichnoneurids had a phytophilous mode of life and fed on generative organs of plants. This mode of life is evidenced by the absence of paranota, by the meso- and metatarsi directed anteriad in imprints, and by the tarsi with pulvilli and a large arolium (Rasnitsyn, 1980). Tococladids have several differences from Ishnoneuridae and are more similar to Eoblattida in wing venation and morphology of the body. In *Opistocladus strictus* Carpenter, 1976 from the Artinskian locality Elmo, United States, the tibiae are directed posteriad, and the pronotum bears narrow paranota (Carpenter, 1976). The forewings of Tococladidae are different from those of Ishnoneuridae in the presence of posterior branches of CuA in the intercubital space, whih makes them similar to Eoblattida. Some authors assigned Tococladidae to Gryllones (Carpenter, 1992; Béthoux *et al.,* 2003; Béthoux, 2007). Indeed, Tococladidae are similar in the morphology of their forewings to Eoblattidae (e.g., *Lobeatta* Béthoux, 2005) and differ from them in the rather proximal branching of M and in CuA having fewer branches. However, Tococladidae are more similar in forewing morphology to the Permian Permitatoridae, which are placed in Hypoperlida (Novokshonov, 1999). Permitatorids had homonomous wings (the hindwings of Tococladidae are poorly known) and therefore can hardly be placed in Gryllones. When additional material on the structure of the mouthparts of Tococladidae becomes available, it may help solve the problem of the position of this family. Until then, it appears preferable to assign Tococladidae to Hypoperlida (Aristov, 2014a).

COMPOSITION. 17 extinct families: Eoblattidae Handlirsch, 1906, Carboniferous of North America and Europe; Protophasmatidae Brongniart, 1885, Carboniferous of North America and Europe, Permian of South America; Cacurgidae Handlirsch, 1911, Carboniferous of North and South America, Permian of North America and Europe; Mesorthopteridae Tillyard, 1916, Permian and Triassic of Eurasia, Triassic of Australia and Africa, Jurassic of Asia; Ideliidae M. Zalessky, 1928, Permian and Triassic of Eurasia; Atactophlebiidae Martynov, 1930, Permotermopsidae Martynov, 1937, Permian of Europe; Euryplonidae Martynov, 1940, Permian of North America and Europe; Bardapteridae G. Zalessky, 1944, Permian of Europe; Megakhosaridae Sharov, 1961, Permian of Eurasia and Africa, Triassic of Eurasia; Blattogryllidae Rasnitsyn, 1976, Permian--Jurassic of Eurasia; Daldubidae Storozhenko, 1996, Carboniferous of Asia; Idelinellidae Storozhenko, 1997, Carboniferous of North America, Permian of Europe; Permopectinidae Aristov, 2005, Permian of Eurasia; Soyanopteridae Aristov et Rasnitsyn, 2011; Doubraviidae **fam. n.**, Permian of Europe. One extant family: Grylloblattidae, distributed in Canada, the United States, Russia, China, North and South Korea, and Japan.

Key to families of the order Eoblattida

1 (32) Wings present.
2 (19) CuA with posterior branches in intercubital space.
3 (16) M_5 present or base of M fused with CuA.
4 (5) SC ending on R .... Eoblattidae Handlirsch, 1906.
5 (4) SC ending on C.
6 (7) M dividing into MA and MP near wing middle or more distally .... Cacurgidae Handlirsch, 1911
7 (6) M dividing into MA and MP in basal third of wing.
8 (9) M_5 diverging from MP .... Daldubidae Storozhenko, 1996
9 (8) M_5 diverging from stem M .
10 (13) Costal space at base of RS wider than subcostal space.
11 (12) CuA not dividing into CuA_1 and CuA_2 ..... Permotermopsidae Martynov, 1937
12 (11) CuA divided into CuA_1 and CuA_2 .... Doubraviidae Aristov, **fam. n.**
13 (10) Costal space at base of RS narrower than or equal in width to subcostal space.
14 (15) M_5 present or M diverging from M+CuA in one stem .... Megakhosaridae Sharov, 1961
15 (14) Base of M fused; CuA, MA and MP diverging from M+CuA in separate stems .... Blattogryllidae Rasnitsyn, 1976
16 (3) M_5 absent; base of M not fused with CuA.
17 (18) CuA forming posterior comb of branches, with gradual transition to anterior comb .... Ideliidae M. Zalessky, 1928
18 (17) CuA branching irregularly .... Bardapteridae G. Zalessky, 1944
19 (2) CuA without posterior branches in intercubital space.
20 (25) SC ending on R.

21 (22) M_5 present .... Protophasmatidae Brongniart, 1885
22 (21) M_5 absent.
23 (24) Head comparable in size to pronotum; interradial space not dilated .... Idelinellidae Storozhenko, 1997
24 (23) Head much larger than pronotum; interradial space strongly dilated .... Soyanopteridae Aristov et Rasnitsyn, 2011
25 (20) SC ending on C.
26 (27) Base of M fused with CuA .... Euryptilonidae Martynov, 1940
27 (26) Base of M not fused with CuA.
28 (29) MP starting branching near its base .... Atactophlebiidae Martynov, 1930
29 (28) MP starting branching at considerable distance from its base.
30 (31) Branches of MP and CuA fine, disappearing among crossveins .... Permopectinidae Aristov, 2005
31 (30) Branches of MP and CuA reaching posterior wing margin .... Mesorthopteridae Tillyard, 1916
32 (1) Wings absent .... Grylloblattidae Walker, 1914

Family Eoblattidae Handlirsch, 1906

Eoblattidae Handlirsch, 1906-1908: 155; 1911: 353; 1919: 50; 1920: 158; 1922: 99; Laurentaux, 1953: 448; Sharov, 1962: 118; Langiaux & Parriat, 1974: 65; Rasnitsyn, 1980: 138; Carpenter, 1992: 129; Rasnitsyn, 2002: 258; Aristov, 2012: 32.

Type genus: *Eoblatta* Handlirsch, 1906.

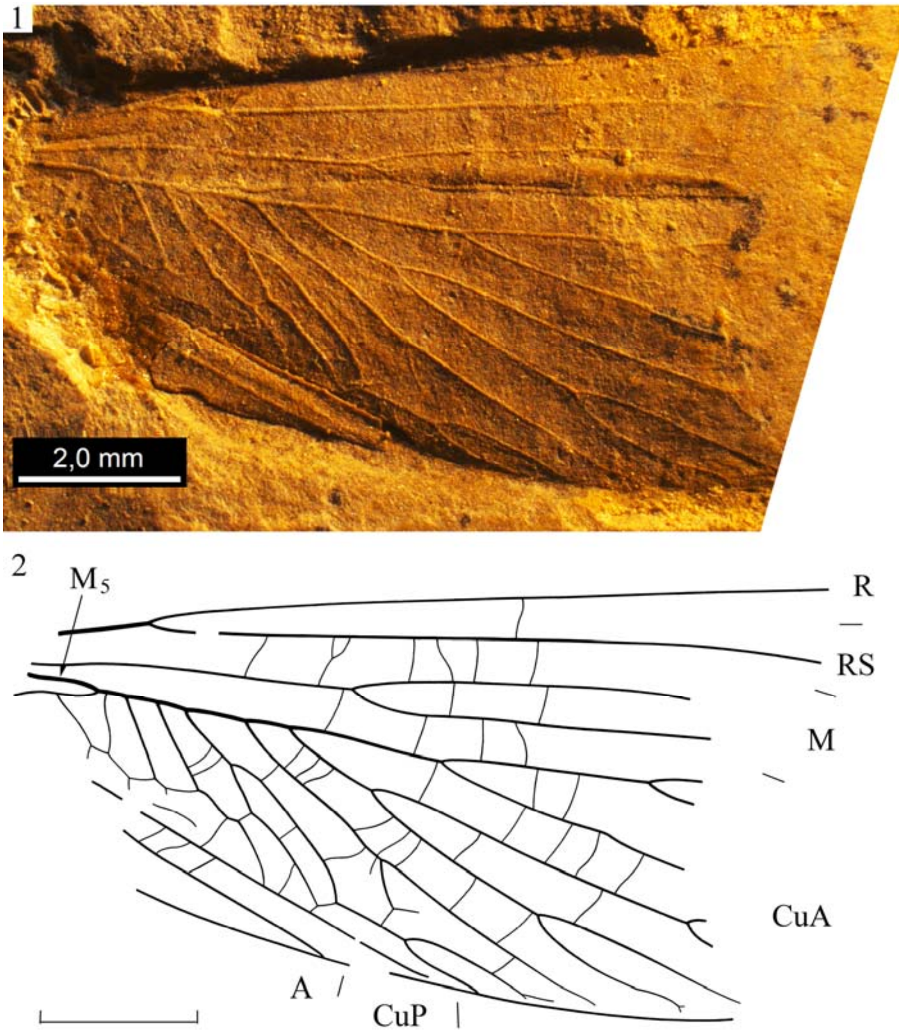
DIAGNOSIS. Head prognathous, with medium-sized eyes and ocelli. Paranota of pronotum without notch on anterior margin (except in *Anegertus* Handlirsch, 1911). Metacoxae set widely apart; meso- and metatibiae directed anteriad. Apices of protibiae with armature; all tarsi three-segmented, without arolium. Forewing with costal space at base of RS wider than subcostal space; SC ending on R. RS beginning in basal quarter of wing (except in *Lobeatta* Béthoux, 2005), interradial space narrowed (except in *Lomovatka* gen. n.). M_5 present; M starting branching distal to base of RS near or distal to wing middle (except in *Lomovatka*). CuA with posterior branches in intercubital space, starting irregularly branching in its basal quarter. Clavus present.

COMPOSITION. Four genera: *Eoblatta* Handlirsch, 1906 from Commentry (France, Allier; Upper Carboniferous, Stephanian Stage B–C) and Montceau-les-Mines (France, Burgundy; Upper Carboniferous, Stephanian Stage B); *Anegertus* Handlirsch, 1911; *Lobeatta* Béthoux, 2005 (Mazon Creek, United States, Illinois; Upper Carboniferous, Desmoinesian Stage) and *Lomovatka* gen. n. from Lomovatka (Ukraine, Lugansk Region; Upper Carboniferous, Kasimovian Stage).

Genus *Lomovatka* Aristov, gen. n.

Type species: *Lomovatka udovichenkoi* sp. n., here designated.

DIAGNOSIS. RS beginning in basal quarter of wing; interradial space not narrowed. M_5 long, S-shaped, M dividing into branches in basal third of wing.



Figs 1, 2. Forewing of *Lomovatka udovichenkovi* Aristov, gen. et sp. n., holotype PIN, No 1866/7. 1 – general appearance; 2 – reconstruction. Scale bar 2 mm.

SPECIES INCLUDED. Type species from Lomovatka locality (Ukraine, Lugansk Region; Kasimovian Stage).

COMPARISON. The new genus is especially similar to *Lobeatta* Béthoux, 2005 from the Desmoinesian locality Mazon Creek, Illinois, United States (Béthoux, 2005; 2008a). *Lomovatka* gen. n. is distinguished from that genus in the interradial space which is not narrowed, long M_5, and M branching rather proximally, in basal third of wing.

ETYMOLOGY. From the Lomovatka locality. Gender feminine.

Lomovatka udovichenkoi **Aristov, sp. n.**
Figs 1, 2

MATERIAL. Holotype PIN, No 1866/7, positive imprint of forewing fragment; Ukraine, Lugansk Region, Popasnaya District, left bank of the Lomovatka River, old sandstone quarry in the Kartanash landscape unit 0.8 km SSE of outskirts of Kalinovo village, Lomovatka locality; Upper Carboniferous, Kasimovian Stage, Upper Isaeva Fm.; in Borissiak Paleontological Institute, Russian Academy of Sciences (PIN).

DESCRIPTION. RS proximal to wing middle simple, branches of M without bifurcations. Posterior branch of M situated on concave area of membrane. CuA with two posterior branches ending among crossveins. CuA branching irregularly, with over 10 branches reaching posterior margin of wing. CuP straight; anal area rather small; A_1 simple. Crossveins simple and forming double row of cells in intercubital space.

MEASUREMENTS. Forewing length about 20 mm.

ETYMOLOGY. In honor of the geologist and paleontologist N.I. Udovichenko (Shevchenko Lugansk National Pedagogical University, Lugansk, Ukraine).

Family Protophasmatidae Brongniart, 1885

Protophasmida Brongniart, 1885: 59.

Protophasmatidae Carpenter, 1992: 130 (*nom. correct. pro* Protophasmida Brongniart, 1885); Rasnitsyn, 2002: 258; Béthoux, 2003: 57.

Protophasmidae Brongniart, 1893: 423; Handlirsch, 1906-1908: 153; Lameere, 1917: 170; Handlirsch, 1919: 50; 1920: 157; Laurentiaux, 1953: 449; Sharov, 1962: 117; Langiaux & Parriat, 1974: 66.

Taiophlebiidae Martins-Neto, Gallego, Brauckmann & Cruz, 2007: 96, **syn. n.**

Type genus: *Protophasma* Brongniart, 1879.

DIAGNOSIS. Head hypognathous (except in *Ischnoptera* Béthoux et Nel, 2005), with rather small eyes. Paranota of pronotum narrow, not protruding anteriad. Meso- and metatibiae directed anteriad (possibly except in *Nosipteron* Béthoux et Poschmann, 2009); tibiae without armature; tarsi four-segmented (Rasnitsyn, 2002, fig. 359), with rather small arolium. Forewing with costal space without precostal lobe (except in *Permeoblatta* Rasnitsyn et Aristov, 2010). Costal space at base of RS wider than subcostal space; SC ending on R or on its anterior branch (in *Permeoblatta* Rasnitsyn et Aristov, 2010). RS beginning in basal third of wing; interradial space narrowed basally (in *Protophasma* Brongniart, 1879) or over its entire length (except in *Pintopinna* gen. n.). M_5 present; M starting branching near wing middle or in basal half of wing (except in *Protophasma*) distal to base of RS. CuA without posterior branches, beginning branching more or less irregularly in basal third. Clavus present.

COMPOSITION. Eight genera: *Protophasma* Brongniart, 1879 from Mazon Creek (United States, Illinois; Upper Carboniferous, Desmoinesian Stage), Piesberg

(Germany, Lower Saxony; Upper Carboniferous, Westphalian Stage D), and Commentry (France, Allier; Upper Carboniferous, Stephanian Stage B–C); *Cacurgulopsis* Pinto et Adami-Rodrigues, 1995 from Boituva (Brazil, São Paulo state; Lower Permian, Sakmarian Stage); *Ischnoptera* Béthoux et Nel, 2005 from Commentry (France, Allier; Upper Carboniferous, Stephanian Stage B–C); *Nectoptilus* Béthoux, 2005 from Mazon Creek; *Taiophlebia* Martins-Neto, 2007 from Taio (Brazil, Santa Catarina state; Lower Permian, Sakmarian Stage); *Nosipteron* Béthoux et Poschmann, 2009 from Nierdermoschel (Germany, Mainz; Lower Permian, Asselian Stage); *Permeoblatta* Rasnitsyn et Aristov, 2010 from Isady (Russia, Vologda Region; Upper Permian, Severodvinian Stage); and *Pintopinna* gen. n. from Boituva (Brazil, São Paulo state; Lower Permian, Sakmarian Stage).

NOTES. The diagnostic characters provided for the family Taiophlebiidae (which includes *Taiophlebia* and *Cacurgulopsis*) were “fore wing with ScP and RA distally fused and RP multi-branched” and “RP origin at 1/5 of the wing base” (Martins-Neto *et al.,* 2007: 96). Since these characters (widespread among Eoblattida) are clearly insufficient to establish a separate family, and the genera *Cacurgulopsis* and *Taiophlebia* show no considerable differences from *Pintopinna,* these genera are assigned here to Protophasmatidae, and the family Taiophlebiidae is synonymized with Protophasmatidae.

The genera *Nectoptilus* and *Nosipteron* were described in Archaeorthoptera without specifying the family and considered close to “lobeattid insects” (Béthoux, 2005; Béthoux & Poschmann, 2009). These two genera are distinguished from that group (which includes *Lobeatta* Béthoux, 2005 and others) by the irregularly dividing CuA without posterior branches. Based on this character and SC ending on R, these genera are assigned here to Protophasmatidae. The genus *Permeoblatta* is transferred from the family Idelinellidae because of the present M_5, which is not found in Idelinellidae (see below). The genus *Cacurgulopsis* was described in the family Cacurgidae, order Protorthoptera (Pinto et Adami-Rodrigues, 1995); this genus is distinguished from cacurids by SC ending on R and by CuA pectinate anteriad. *Ischnoptera* was described in Archeorthoptera without specifying the family and considered close to Cnemidolestidae (Béthoux & Nel, 2005); this genus is distinguished from Cnemidolestidae by MP present and by CuA pectinate antereiad. Both genera are transferred to Protophasmatidae based on the latter character.

Protophasma multidiffusa (Brauckmann et Nerd, 2005), comb. nov.

Heterologellus (?) *multidiffusus* Brauckmann & Nerd, 2005: 29, Abb. 5; Taf. 1, Fig. 2.

MATERIAL. Holotype F8 in Sammlung des Finders und Amateur-Paläontologen of Michael Sowiak (Osnabrück, Germany).

NOTES. In addition to two species from Commentry and Mazon Creek (Béthoux, 2003; Béthoux & Schnider, 2010), the species *Heterologellus* (?) *multidiffusus* Brauckmann et Nerd, 2005 from Piesberg is also assigned here to the genus *Protophasma*.

In the type species of *Heterologellus*, *H. teichmuellerae* Schmidt, 1962, CuA is pectinate posteriad (Schmidt, 1962), whereas in the species in question, as well as in the type species of the genus *Protophasma, P. dumasi* (Béthoux, 2003), CuA is divided into two branches, and the anterior branch is pectinate anteriad (Brauckmann & Nerd, 2005). Therefore, the species is treated here as *Protophasma multidiffusum* (Brauckmann et Nerd, 2005), comb. n.; it is distinguished from *P. dumasi* by M dividing rather proximally, proximal to the middle.

Genus *Pintopinna* Aristov, gen. n.

Type species: *Paranarkemina martinsnetoi* Pinto, 1999, here designated.

DIAGNOSIS. Forewing with costal space at base of RS 2.5 times as wide as subcostal space. M_5 short, joining CuA proximal to its division into branches; M starting branching distal to middle of wing; its anterior branch fused with RS. CuA S-shaped distal to M_5, branching into posterior comb with gradual transition to anterior comb. Apex of A_1 fused with A_2.

SPECIES INCLUDED. Type species only.

COMPARISON. *Pintopinna* is especially similar to *Nosipteron* and differs from it in M rather distally branching and in CuA partly fused with RS, curved, and forming posterior comb with a gradual transition to the anterior comb.

ETYMOLOGY. In memory of the paleoentomologist D. Pinto and the Latin *pinna* (wing). Gender feminine.

NOTES. *P. martinsnetoi* was described in the genus *Paranarkemina* (Pinto, 1999), which I assign to Cnemidolestidae (Cnemidolestida; Aristov, 2014). The genus *Pintopinna* is placed here in Protophasmatidae based on MP not reduced and CuA irregularly branching. In Cnemidolestidae MP is weak, not reaching wing margin, or absent, and CuA forms two combs of branches directed towards each other (Aristov, 2014).

Pintopinna martinsnetoi **(Pinto, 1999), comb. n.**

MATERIAL. Holotype: UFRGS, No MP-I-5279, imprint of forewing; Brazil, São Paulo state, Boituva municipality, Boituva locality; lower Permian Sakmarian Stage, Itararé Group, Boituva Fm.; in Universidade Federal do Rio Grande do Sul, Brazil. Not examined.

Family Cacurgidae Handlirsch, 1911

Cacurgidae Handlirsch, 1911: 324; Pruvost, 1919: 124; Handlirsch, 1920: 152; 1922: 89; Pruvost, 1930: 157; Sharov, 1962: 122; Richardson, 1956: 33; Rasnitsyn, 1980a: 31; 1980b: 20; Pinto, 1990: 7; Carpenter, 1992: 120; Kukalová-Peck & Brauckmann, 1992: 2463; Pinto & Adami-Rodrigues, 1995: 53; Storozhenko, 1998: 44; Pinto & Adami-Rodrigues, 1999: 122; Würdig *et al.*, 1999: 180; Béthoux & Nel, 2002: 15; Rasnitsyn, 2002: 259; Schluter, 2003: 351; Béthoux; 2006: 30; Aristov, 2012: 34.

Type genus: *Cacurgus* Handlirsch, 1911.

DIAGNOSIS. Head prognathous, with large eyes and very long antennae. Paranota of medium width, without notch on anterior margin. Legs elongatede; meso- and metatibiae directed anteriad; apices of tibiae without armature. Forewing with costal space at base of RS wider than or as wide as subcostal space; SC ending on C. RS beginning in basal third of wing; interradial space not narrowed. M_5 present;

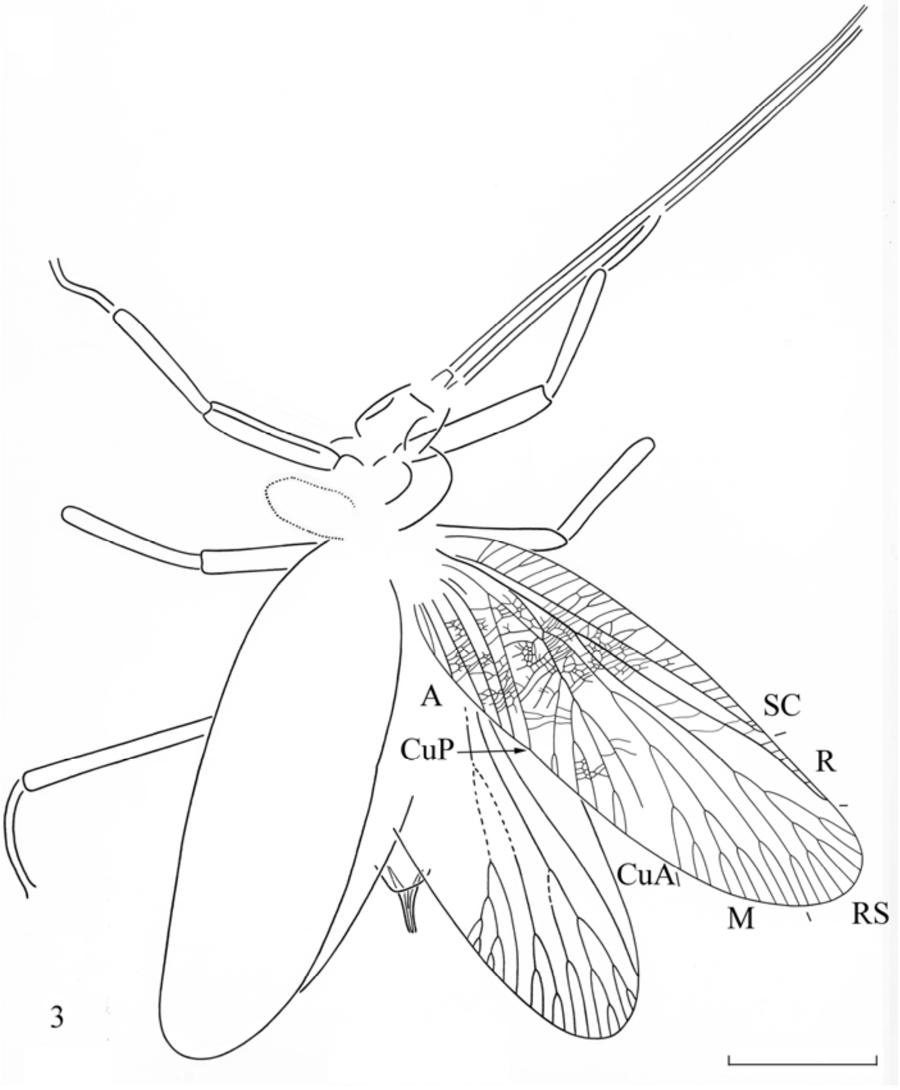


Fig. 3. *Kochopteron hoffmannorum* Brauckmann, 1984, reconstruction based on drawing of holotype No H-3 (Brauckmann, 1991: fig. 78), photograph of specimen WMf. N P 26093 (Ilger & Brauckmann, 2008: fig. 1), drawing of specimen AKG 1516 (Ilger & Brauckmann, 2012: fig. 8) and specimen WMf.N P.31712 (Ilger, 2011: fig. 12). Scale bar 10 mm.

M starting branching distal to base of RS, in wing middle or more distally. CuA with posterior branches, starting irregularly branching in basal third (except in *Kochopteron* Brauckmann, 1984), with distal branch sometimes desclerotized (in *Ideliopsis* Carpenter, 1948 and *Kitshuga* Aristov, 2012). Clavus absent (except in *Cacurgus* Handlirsch, 1911 and *Kochopteron* Brauckmann, 1984), ovipositor long.

COMPOSITION. Five genera: *Cacurgus* Handlirsch, 1911 from Mazon Creek (United States, Illinois; Upper Carboniferous, Desmoinesian Stage); *Ideliopsis* Carpenter, 1948 from Castle Hollow (United States, Texas; Lower Permian, Leonardian Stage); *Kochopteron* Brauckmann, 1984 from Hagen-Vorhalle (Germany, North Rhine-Westphalia; Upper Carboniferous, Namurian Stage B; Fig. 3); *Kitshuga* Aristov, 2012 from Isady (Russia, Vologda Region; Upper Permian, Severodvinian Stage); and *Suksunus* gen. n. from Chekarda (Russia, Perm Region; Lower Permian, Kungurian Stage). In addition, one undescribed genus from the Upper Carboniferous of Argentina has been tentatively assigned to Cacuridae (Aristov, 2012).

Genus *Suksunus* Aristov, gen. n.

Type species: *Suksunus bicodex* sp. n., here designated.

DIAGNOSIS. Costal space in basal third of forewing 1.5 times as wide as subcostal space. RS beginning in basal quarter of wing; interradial space strongly narrowed. M starting branching in basal third of wing, proximal to first bifurcation of CuA. CuA starting branching at its middle; CuP convex.

SPECIES INCLUDED. Type species only.

COMPARISON. The new genus is especially similar to *Kochopteron* and differs from it in more proximal base of RS and first bifurcation of M. In *Kochopteron,* RS begins at the end of the basal third, and M starts branching in the middle of the wing.

ETYMOLOGY. From Suksun District, Perm Region. Gender masculine.

Suksunus bicodex **Aristov, sp. n.**

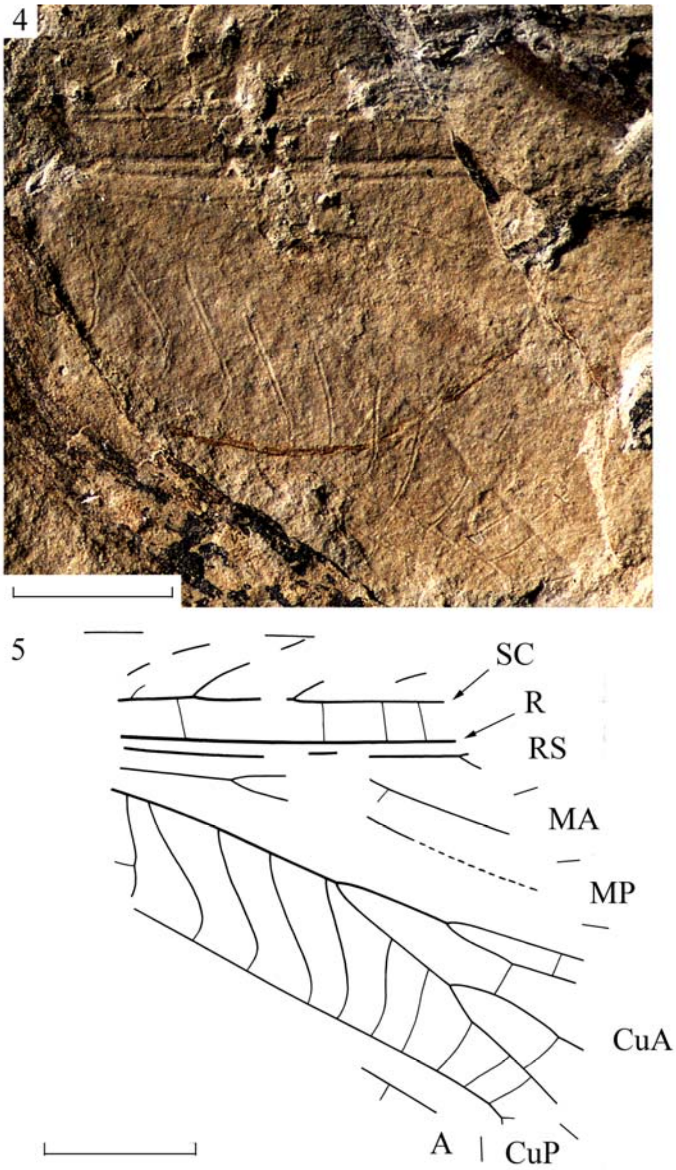
Figs 4, 5

MATERIAL. Holotype PIN, No 1700/803, positive imprint of forewing fragment; Russia, Perm Region, Suksun District, left bank of the Sylva River downstream of the mouth of the Chekarda River, Chekarda locality; Lower Permian, Kungurian Stage, Koshelevka Fm.; in PIN.

DESCRIPTION. SC convex, with sparse S-shaped anterior branches. RS starting branching proximal to wing middle, M starting branching distal to base of RS; posterior branch desclerotized. CuA with dense S-shaped posterior branches, dichotomizing, with more than four branches; CuP slightly curved near apex. Crossveins simple.

MEASUREMENTS. Forewing length about 34 mm.

ETYMOLOGY. From the Latin *bicodex* (arbitrary combination of letters).



Figs 4, 5. Forewing of *Suksunus bicodex* Aristov, gen. et sp. n., holotype PIN, No 1700/803. 4 – general appearance; 5 – reconstruction. Scale bar 1 mm.

Family Mesorthopteridae Tillyard, 1916

Mesorthopteridae Tillyard, 1916: 14; 1922: 447; Riek, 1956: 105; Sharov, 1962: 124; Rasnitsyn, 1980: 153 (partim); Storozhenko, 1996b: 115; 1997a: 15; 1997b: 65; 1998: 131;

2002: 280; Aristov *et al.*, 2011: 41; Aristov & Storozhenko, 2013: 8; Aristov, 2013b: 761; 2014b: 489; Aristov & Rasnitsyn, 2015: 21; Aristov, 2015a: 88; Shcherbakov, 2015: 190.

Ideliidae: Riek, 1954: 161 (partim).

Type genus: *Mesorthopteron* Tillyard, 1916.

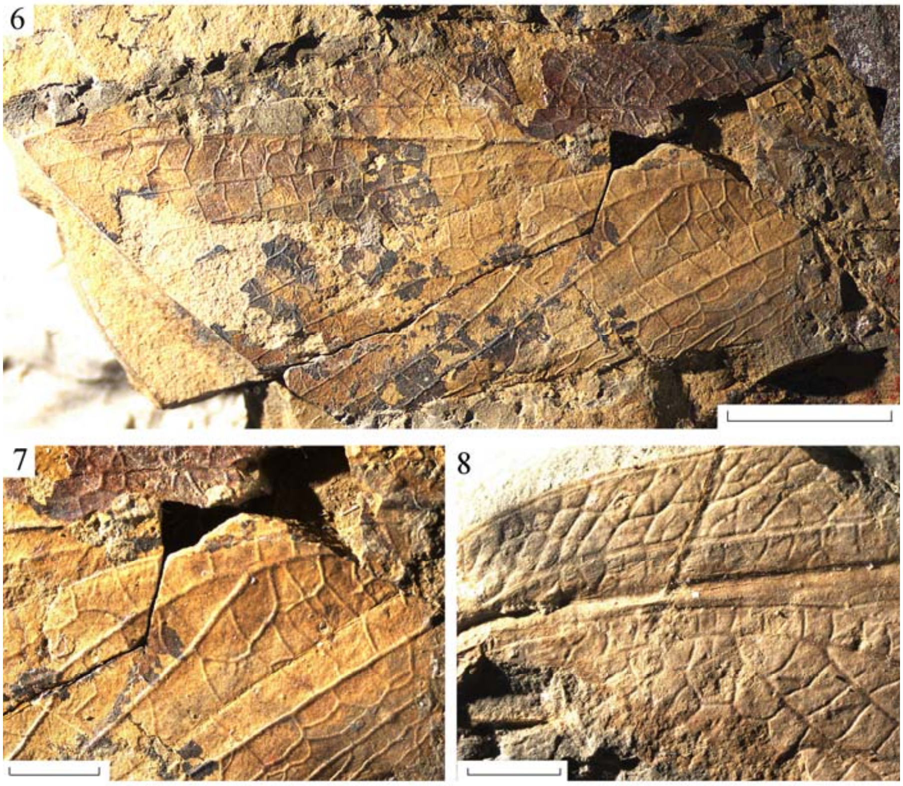
DIAGNOSIS. Head pro- or hypognathous with small eyes, without ocelli, and with short antennae. Paranota wide, without notch on anterior margin. Meso- and metatibiae directed posteriad. Apices of tibiae without armature; tarsus five-segmented with large arolium. Forewing with costal space at base of RS in most cases wider than subcostal space; SC ending on C. RS beginning in basal half of wing; interradial space not narrowed. M_5 absent; M starting branching proximal to or near base of RS in basal third of wing (except in *Mesorthopterina* Storozhenko, 1996). CuA without posterior branches (except in some specimens of *Paridelia pusilla* Sharov, 1961), starting branching in its basal quarter, in most cases branching irregularly or pectinate. Clavus absent (except in *Sharovites* Aristov et Storozhenko, 2013). Hindwing with CuA with posterior branches in intercubital space (*Parastenaropodites* Storozhenko, 1996). Ovipositor short, strong; cerci short.

COMPOSITION. 10 genera: *Mesorthopteron* Tillyard, 1916 from Denmark Hill and Fletcher (Australia, Queensland, and South Africa, Eastern Cape Province, respectively; Upper Triassic, Carnian Stage); *Austroidelia* Riek, 1954 from Beacon Hill (Australia, New South Wales; Middle Triassic, Anisian Stage) and Madygen (Kyrgyzstan, Osh Region; Middle Triassic, Ladinian Stage); *Paridelia* Sharov, 1961 from Kaltan (Russia, Kemerovo Region; Middle Permian, Kazanian Stage); *Parastenaropodites* Storozhenko, 1996 from Chekarda (Russia, Perm Region, Lower Permian, Kungurian Stage); Vorkuta (Russia, Komi Republic, Lower Permian, Ufimian Stage), Soyana (Russia, Arkhangelsk Region, Middle Permian, Kazanian Stage), Karaungir (Kazakhstan, East Kazakhstan Region, Middle Permian, Urzhumian Stage), Kulchumovo (Russia, Orenburg Region, Upper Permian, Severodvinian Stage), Isady (Russia, Vologda Region, Upper Permian, Severodvinian Stage), and Madygen; *Mesoidelia* Storozhenko, 1996 from Isady and Madygen; *Mesorthopterina* Storozhenko, 1996 from Kyzyl-Tam (Kazakhstan, Ketmen Mountain Range; Upper Triassic, Carnian Stage); *Sharovites* Aristov et Storozhenko, 2013 from Madygen, *Tshermyaninus* Aristov, 2014 and *Permorthopteron* Aristov, 2014 from Isady; and *Taskanatus* gen. n. from Karaungir.

NOTE. The genus *Paridelia* was described in the family Ideliidae (Sharov, 1961) and subsequently transferred to Kortshakoliidae (Storozhenko, 1997a). After the synonymization of Kortshakoliidae under Permotermopsidae (see below), I assigned the genus *Paridelia,* which is rather different from *Kortshakolia* Sharov, 1961, to Mesorthopteridae. *Paridelia pusilla* Sharov, 1961 is similar to *Mesoidelia gorochovi* Aristov, 2013 from the Severodvinian locality Isady (Aristov, 2013). *Paridelia pusilla* is distinguished from latter by the convex SC, RS beginning distal to the basal third of the wing, and CuA pectinate posteriad (Fig. 6-8). In addition, specimens of *Paridelia* typically have rudimentary posterior branches of CuA, which are lost among the somewhat finer crossveins in the intercubital space (Fig. 7).

This character is subject to individual variation: in another specimen of the same species all crossveins at the base of the intercubital space are equal in thickness (Fig. 8).

The genus *Paleomesorthopteron* Aristov, Grauvogel-Stamm et Marchal-Papier, 2011, from the Vosges (France, Alsace and Lorraine; Middle Triassic, Anisian Stage) was described as Mesorthopteridae is transferred into family Alexarasniidae of the order Embiodea (*sensu* Shcherbakov, 2015).



Figs 6-8. Forewings of *Paridelia pusilla* Sharov, 1961. 6, 7 – holotype PIN, No 600/501; 8 – specimen PIN, No 1197/250. Scale bar in fig. 6 – 5mm, in figs 7 and 8 – 2 mm.

Genus *Taskanatus* Aristov, gen. n.

Type species: *Alicula asiatica* Storozhenko, 1997, here designated.

DIAGNOSIS. Costal space at base of RS 1.5 times as wide as subcostal space. RS beginning near middle of wing. M not running very close to R, dividing into MA and MP proximal to base of RS. Base of CuA curved; CuA not S- shaped, forming posterior comb with branches finer than stem, anterior branch forming anterior comb. Intercubital space dilated basally. Crossveins forming archedictyon.

SPECIES INCLUDED. Type species only.

9

10

Figs 9, 10. Forewing of *Taskanatus asiaticus* (Storozhenko, 1997), comb. n. 9 – holotype PIN, No 2781/248; 10 – fragment of counterpart of holotype. Scale bar in fig. 9 – 3 mm, in fig. 10 – 1 mm.

COMPARISON. The new genus is especially similar to *Mesoidelia* and differs from it in the CuA forming posterior comb with gradual transition to anterior comb and in the basally dilated intercubital space.

ETYMOLOGY. From the Kazakh *tas* (stone) *kanat* (wing). Gender masculine.

NOTE. *Alicula asiatica* Storozhenko, 1997 was erroneously transferred from the genus *Alicula* Schlechtendal, 1913 of the family Aliculidae (Storozhenko, 1997a) to the genus *Metidelia* Martynov, 1937 of the family Ideliidae (Aristov, 2004b). In spite of the similar branching of CuA (which forms a posterior comb with transition to an anterior comb), this species cannot be assigned to Ideliidae. In this species, none of the posterior branches of CuA are either ending on CuP or lost in the intercubital space. This combination of characters allows assigning this species to a new monotypic genus, *Taskanatus,* in the family Mesorthopteridae.

Taskanatus asiaticus **(Storozhenko, 1997), comb. n.**

Figs 9, 10

MATERIAL. Holotype PIN, No 2781/248, positive and negative imprint of basal part of wing; Kazakhstan, East Kazakhstan Region, Zaysan District, left bank of the Karaungir River 600 m downstream of the Maichat River, Karaungir II locality; Middle Permian, Urzhumian Stage (Rasnitsyn *et al.,* 2013), Maichat Fm.; in PIN, examined.

Family Ideliidae M. Zalessky, 1928

Ideliidae M. Zalessky, 1928: 301; 1929: 21; Sharov, 1961: 171; 1962: 119; Rasnitsyn, 1980: 152; Storozhenko, 1992b: 22, 38 (partim); Carpenter, 1992: 118; Storozhenko, 1994a: 50; 1997a: 11; 1997b: 64; Novokshonov, 1998: 37; Storozhenko, 1998: 106; 2002: 279; Aristov, 2002: 47; 2004a: 124; 2009a: 42; 2010: 34; Aristov, 2015a: 88.

Rachimentomidae G. Zalessky, 1939: 55 (synonimized by Sharov, 1962: 119).

Mesorthopteridae: Rasnitsyn, 1980: 153 (partim).

Type genus: *Idelia* M. Zalessky, 1928 (= *Stenaropodites* Martynov, 1928).

DIAGNOSIS. Head small, prognathous, with medium-sized eyes, ocelli, and long antennae. Paranota wide, with rather shallow, wide notch on anterior margin. Pterothorax with sternal suture, coxae closely set. Meso- and metatibiae directed posteriad. Tibiae in most cases without armature (in *Sylvidelia* Martynov, 1940 mesotibiae with row of small spines), tarsus five-segmented with large (in *Sylvidelia* very large) arolium. Forewing with costal space at base of RS wider than subcostal space, costal lobe (except in *Rachimentomon* G. Zalessky, 1939) and "C" (possibly except in *Aenigmidelia* Sharov, 1961) absent, SC ending on C. RS beginning in basal half of wing; interradial space not narrowed. M_5 absent (except in *Archidelia* Sharov, 1961); M starting branching proximal to base of RS in basal half of wing. CuA with posterior branches, starting branching in its basal quarter, forming posterior comb of branches, with gradual transition to anterior comb (except in *Tshekardelia* Aristov, 2002). Clavus absent. Ovipositor long and strong, valves of ovipositor in *Rachimentomon* G. Zalessky, 1939 with denticles, cerci short, fusiform.

COMPOSITION. 15 genera: *Stenaropodites* Martynov, 1928 from Soyana, Tikhie Gory, and Kityak (Russia, Arkhangelsk Region, Tatarstan and Kirov Region, respectively; Middle Permian, Kazanian Stage); *Metidelia* Martynov, 1937 from Kargala (Russia, Orenburg Region; Middle Permian, Urzhumian Stage); *Rachimentomon* G. Zalessky, 1939 and *Sylvidelia* Martynov, 1940 from Chekarda (Russia, Perm Region; Lower Permian, Kungurian Stage); *Kolvidelia* G. Zalessky, 1950 from Kolva (Russia, Perm Region; Lower Permian, Ufimian Stage); *Archidelia* Sharov, 1961 and *Aenigmidelia* Sharov, 1961 from Kaltan (Russia, Kemerovo Region; Middle Permian, Kazanian Stage); *Sojanidelia* Storozhenko, 1992 from Chekarda and Vorkuta (Russia, Komi Republic; Lower Permian, Ufimian Stage), Soyana and Kaltan; *Mongoloidelia* Storozhenko, 1992 from Bor Tologoi (Mongolia, East Gobi Province; Middle Permian, Urzhumian Stage); *Pseudoshurabia* Storozhenko, 1996, *Madygenidelia* Storozhenko, 1996, and *Anaidelia* Storozhenko, 1996 from Madygen (Kyrgyzstan, Osh Region; Middle Triassic, Ladinian Stage); *Idelopsina* Storozhenko, 1996 from Madygen and Kenderlyk (Kazakhstan, East Kazakhstan Region; Upper Triassic, Rhaetian Stage); *Tshekardelia* Aristov, 2002 and *Micoidelia* Aristov, 2004 from Chekarda (Russia, Perm Region; Lower Permian, Kungurian Stage).

Family Atactophlebiidae Martynov, 1930

Atactophlebiidae Martynov, 1930a: 952; 1930b: 1131; Sharov, 1962: 130; Rasnitsyn, 1980a: 150, 152; Storozhenko, 1990: 407; Carpenter, 1992: 118; Storozhenko, 1994a: 49; 1997a: 5; 1997b: 63; 1997c: 8; 1998: 72; Novokshonov, 1998: 36; Aristov, 1999: 179; Storozhenko, 2002: 279; Aristov, 2004a: 97; Béthoux *et al*., 2005: 133; Aristov, 2009a: 41; 2015a: 89; 2015b: 1312; Shcherbakov, 2015: 196.

Type genus: *Atactophlebia* Martynov, 1930.

DIAGNOSIS. Pronotum with paranota; meso- and metatibiae directed posteriad. Precostal space absent. Costal space in basal third of forewing as wide as or slightly wider than subcostal space (except in *Issadophlebia*), SC concave (except in some *Atactophlebia*), ending on C. RS beginning in basal half of wing; interradial space not narrowed. M_5 diverging from M or MP, joining CuA near its first bifurcation. M dividing near M_5 or at some distance from it, proximal to base of RS (except in *Malmyzhia*) in basal third of wing; MP starting branching near its base. Anterior branch of MP often desclerotized. CuA without posterior branches, not dividing into CuA_1 and CuA_2 (except in *Issadophlebia*), branching irregularly or forming irregular posterior comb of branches (distal branch sometimes pectinate anteriad) in its basal quarter; posterior branch of CuA simple. CuP simple, concave; clavus absent.

COMPOSITION. Five genera: *Atactophlebia* Martynov, 1928 from Tikhie Gory and Soyana (Russia, Tatarstan and Arkhangelsk Region, respectively; Middle Permian, Kazanian Stage); *Kirkorella* G. Zalessky, 1939 and *Novokhonovus* Aristov et Rasnitsyn, 2015 from Chekarda (Russia, Perm Region; Lower Permian, Kungurian Stage); *Malmyzhia* gen. n. from Kityak (Russia, Kirov Region; Middle Permian, Kazanian Stage); and *Issadophlebia* gen. n. from Isady (Russia, Vologda Region; Upper Permian, Severodvinian Stage).

Genus *Malmyzhia* Aristov, gen. n.

Type species: *Malmyzhia kazanica* sp. n., here designated.

DESCRIPTION. Forewing with preradial space narrow. SC ending proximal to wing middle; RS beginning in basal quarter of wing. M with many branches, starting branching distal to base of RS. CuA forming posterior comb of branches with distal branch pectinate anteriad.

DIAGNOSIS. The new genus is especially similar to *Kirkorella* and differs from it in more proximal base of RS and M starting branching distal to base of RS. In *Kirkorella,* RS begins in the middle of the wing, and M starts branching proximal to the middle of the wing (Storozhenko, 1998).

SPECIES INCLUDED. Type species.

ETYMOLOGY. From Mamlyzh District, Kirov Region. Gender feminine.

Malmyzhia kazanica **Aristov, sp. n.**
Figs 11, 12

MATERIAL. Holotype PIN, No 1366/246, positive and negative imprint of forewing; Russia, Kirov Region, Mamlyzh District, left bank of the Kityak River opposite Bolshoi Kityak village, Kityak locality; Middle Permian, Upper Kazanian Substage, Belebeevo Fm.; in PIN.

DESCRIPTION. Anterior margin of forewing in distal half weakly convex. RS starting branching in distal third of wing, three-branched. MA with simple short bifurcation; MP starting branching rather near its base, five-branched. CuA seven-branched. Anal area rather small.

MEASUREMENTS. Forewing length about 20 mm.

ETYMOLOGY. From the Kazanian Stage.

Genus *Issadophlebia* Aristov, gen. n.

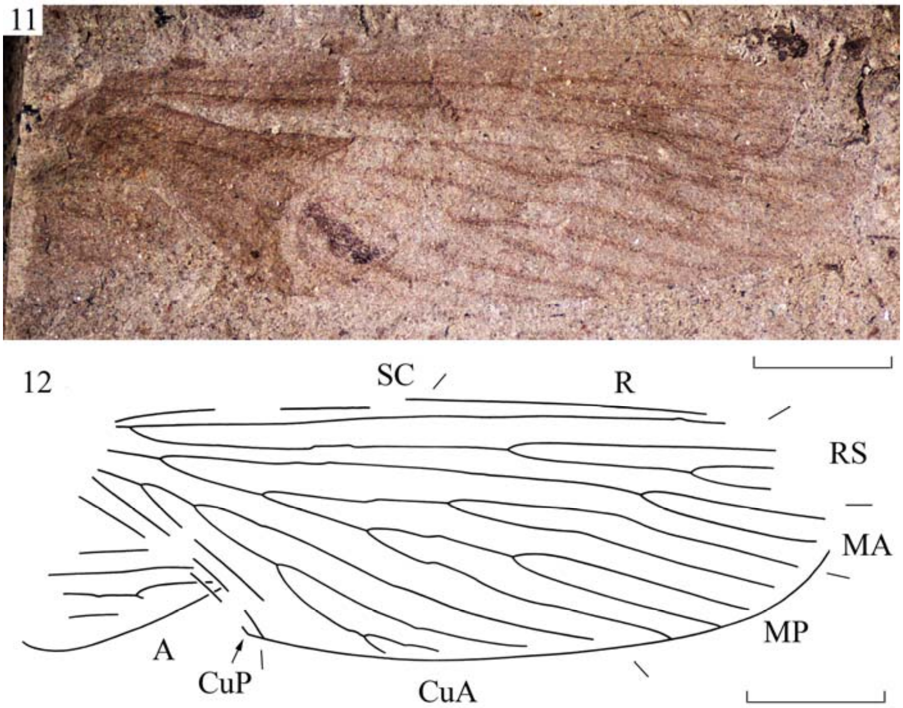
Type species: *Issadophlebia fusa* sp. n., here designated.

DESCRIPTION. Forewing with costal space at base of RS four times as wide as subcostal space. SC reaching intto distal quarter of wing. RS beginning in basal quarter of wing, starting branching in distal quarter of wing. M starting branching proximal to base of RS; MA simple; MP starting branching rather near its base, pectinate posteriad, with stem situated on concave area of membrane. CuA divided into CuA_1, starting branching at its middle, and CuA_2, simple, S-shaped. Distal part of CuP convex, situated on concave area of membrane.

DIAGNOSIS. The new genus is especially similar to *Malmyzhia* gen. n. and differs from it in the wide costal space, MP pectinate posteriad, and CuA divided into CuA_1 and CuA_2. In *Malmyzhia,* the costal space is narrow, and MP and CuA branch irregularly (see above).

SPECIES INCLUDED. Type species.

ETYMOLOGY. From the Isady locality and the generic name *Atactophlebia*. Gender feminine.



11, 12. *Malmyzhia kazanica* Aristov, gen. et sp. n., holotype PIN, No 1366/246, forewing. 11 – general appearance, 12 – reconstruction. Scale bar 3 mm.

Issadophlebia fusa **Aristov, sp. n.**

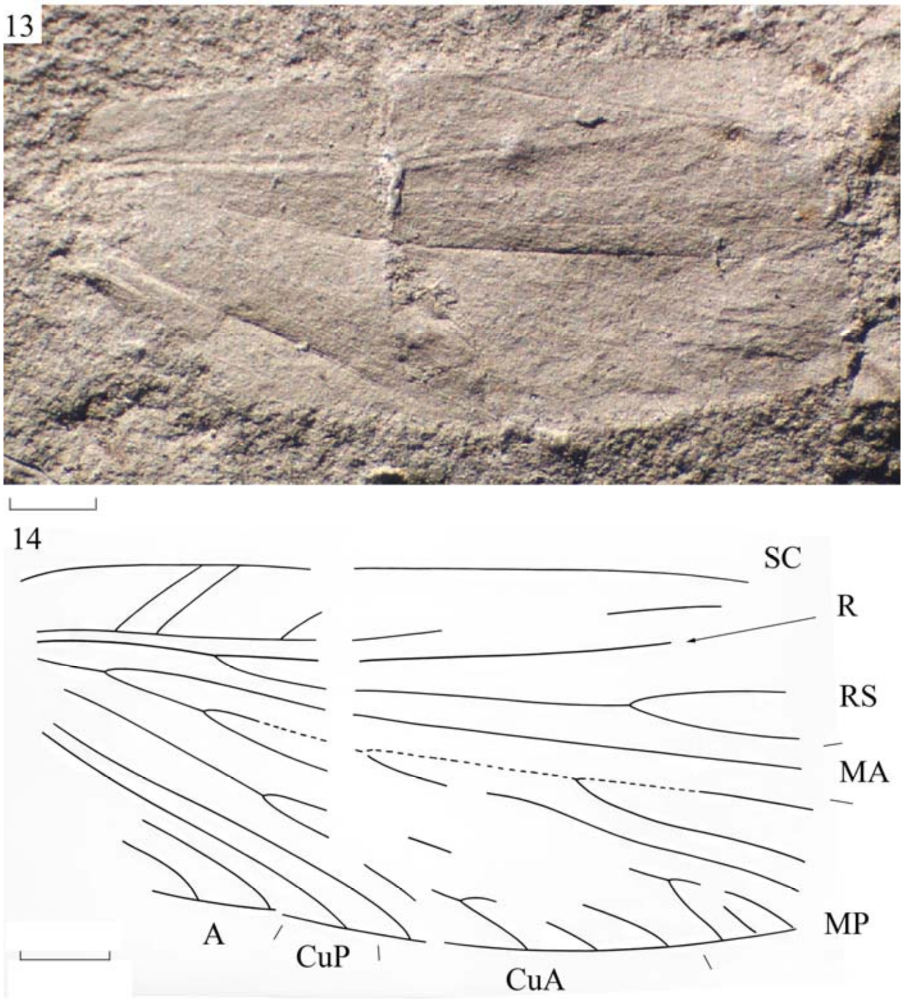
Figs 13, 14

MATERIAL. Holotype PIN, No 3840/3164, positive and negative imprint of forewing fragment; Russia, Vologda Region, Veliky Ustyug District, left bank of the Sukhona River 1 km upstream of Isady village, Isady locality; Upper Permian, Severodvinian Stage, Poldarsa Fm.; in PIN.

DESCRIPTION. Anterior margin of forewing weakly convex, SC with dense and simple anterior branches. RS in distal quarter of wing with two branches. MP with four main branches and probably greater number of apical bifurcations; posterior branch with three ends. CuA_1 branching irregularly, with four ends. Anal area rather small.

MEASUREMENTS. Forewing length about 12 mm.

ETYMOLOGY. Feminine form of the Latin *fusus* (broad).



13, 14. *Issadophlebia fusa* Aristov, gen. et sp. n., holotype PIN, No 3840/3164, forewing. 13 – general appearance; 14 – reconstruction. Scale bar 1 mm.

Family Permotermopsidae Martynov, 1937

Permotermopsidae Martynov, 1937: 84; Sharov, 1962: 119; Carpenter, 1992: 209; Storozhenko, 1997a: 16; 1997b: 30; 1998: 162; 2002: 280; Rasnitsyn *et al*., 2005: 71; Aristov, 2009a: 38; 2013a: 52; 2015b: 1312.

Ideliidae (partim): Sharov, 1962: 119; Storozhenko, 1992: 38; 1997b: 63.

Aliculidae Storozhenko, 1997a: 8 (sinonimized under Permulidae by Aristov & Storozhenko, 2011: 113); Storozhenko, 1997b: 25; 1998: 97; 2002: 279; Aristov, 2004: 105; 2009a: 37.

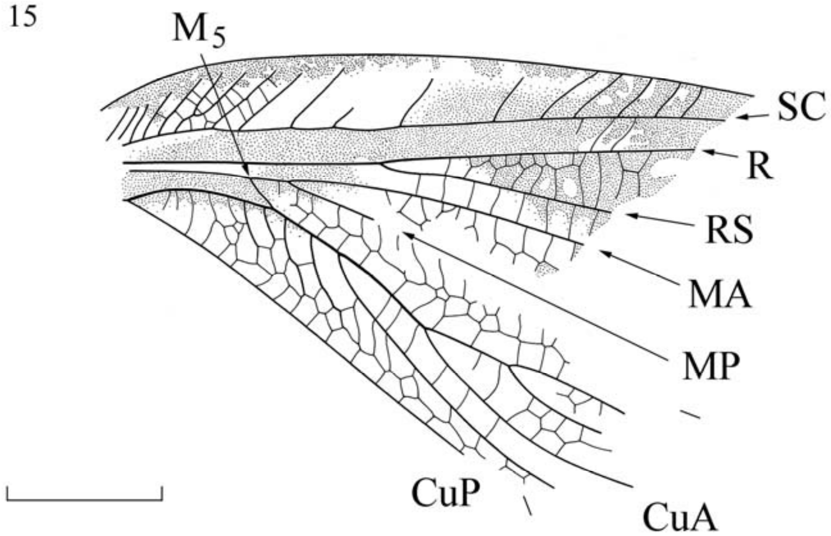
Kortshakoliidae Storozhenko, 1997a: 12; 1997b: 28; 1998: 117; 2002: 279; Aristov, 2009a: 42; 2009b: 21, **syn. n.**

Permulidae Aristov & Storozhenko, 2011: 113; Aristov, 2014: 23, **syn. n.**

Type genus: *Permotermopsis* Martynov, 1937.

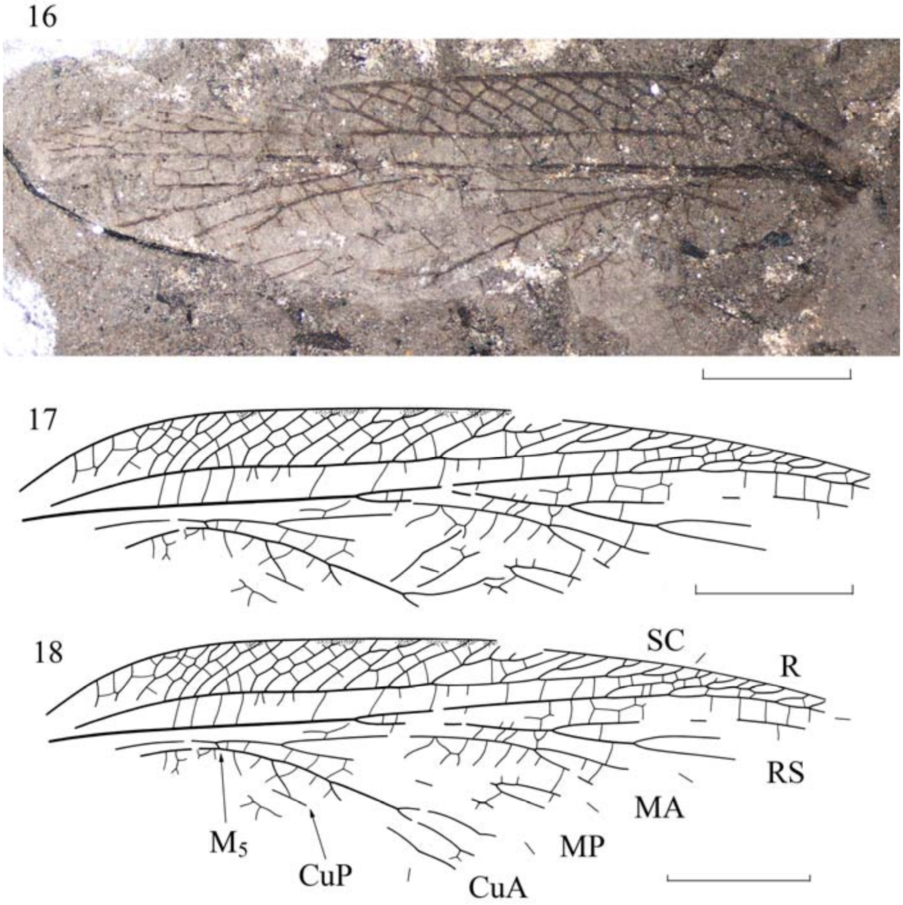
DIAGNOSIS. Forewing with costal space at base of RS wider than subcostal space; SC ending on C. RS beginning in basal half of wing; interradial space not narrowed. M_5 present; M starting branching proximal to base of RS in basal third of wing. CuA with posterior branches and starting branching distal to its basal third (except in *Permofossilis*), pectinate posteriad. Clavus absent.

15



15. Forewing of *Permula lebachensis* (Schlechtendal, 1913), original drawing based on photograph of holotype NVB, No 50, 51 (Gutörl, 1934: Tabl. 16, fig. 4). Scale bar 5 mm.

COMPOSITION. Seven genera: *Permotermopsis* Martynov, 1937 from Soyana (Russia, Arkhangelsk Region; Middle Permian, Kazanian Stage); *Permula* Handlirsch, 1919 from Lebach (Germany, Saarland; Lower Permian, Asselian Stage; Fig. 15); *Kortshakolia* Sharov, 1961 from Korchakola (Russia, Kemerovo Region; Middle Permian, Kazanian Stage; Figs 16–18); *Idelina* Storozhenko, 1992 from Tikhie Gory and Kityak (Russia, Tatarstan and Kirov Region; Middle Permian, Kazanian Stage); *Khosaridelia* Storozhenko, 1992 from Vorkuta (Russia, Komi Republic; Lower Permian, Ufimian Stage); *Permofossilis* Aristov, 2013 from Isady (Russia, Vologda Region; Upper Permian, Severodvinian Stage) and *Belebey* gen. n. from Kityak (Russia, Kirov Region; Middle Permian, Kazanian Stage).



16–18. Forewing of *Kortshakolia ideliformis* Sharov, 1961, holotype PIN, No 1213/1. 16 – general appearance; 17, 18 – reconstruction. Scale bar 5 mm.

NOTES. The family Permulidae Aristov et Storozhenko, 2011 of the order Grylloblattida was erected for the genus *Permula* Handlirsch, 1919 and several other Permian genera: *Sojanopermula*, *Neprotembia*, *Elmopterum*, *Tshepanichoptera*, *Kazanalicula*, and *Mezenalicula* (Aristov & Storozhenko, 2011). The type species of the genus *Permula*, *P. lebachensis* (Schlechtendal, 1913), was described from the locality Steinbach bei Lebach-Saar (Germany, Hesse; Lower Permian, Asselian Stage). A photograph of the holotype provided by Gutörl (1934, Tabl. 16, fig. 4) is of higher quality than the photograph provided in the original description (Schlechtendal, 1913, Tabl. 2, figs. 10a, 10b) and shows some characters found neither in other species of the genus nor in the other genera formerly assigned to Permulidae. *P. lebachensis* has wide costal and interradial spaces, strong M_5, and CuA dividing rather proximally and pectinate posteriad, with posterior branches in the intercubital space (Fig. 15), whereas in the other permulids posterior branches of CuA are unknown. This combination of characters is found only in the family Permotermopsidae of the order Eoblattida. Among permotermopsids, the species especially similar to *P. lebachensis* is *Khosaridelia martynovi* Storozhenko, 1992 from Vorkuta (Russia, Komi Republic; Ufimian Stage; Storozhenko, 1992). The differences between the two genera are limited to the more basal bifurcation of RS and shorter M_5 in *K. martynovi*. Therefore, the genus *Permula,* including only the type species, is transferred to Permotermopsidae, with which the family Permulidae is synonymized. Two other species formerly included in this genus, *Permula tshekardensis* (Aristov, 2004) and *P. minor* (Aristov, 2004), are transferred back to the genus *Sojanopermula*, in which they were originally described (Aristov, 2004a); *P. edemskii* Aristov et Storozhenko, 2011 is also transferred to the genus *Sojanopermula*. The genera *Sojanopermula*, *Neprotembia*, *Elmopterum*, *Tshepanichoptera,* and *Kazanalicula* were transferred to family Sylvabestiidae of the order Cnemidolestida (Aristov, 2014). The genus *Mezenalicula* Aristov et Storozhenko, 2011 from Soyana was described in the family Permulidae (Aristov & Storozhenko, 2011) and was not transferred to Sylvabestiidae by me (Aristov, 2014a). Re-examination of the only species of this genus, *M. connata,* using additional material shows that it is similar in wing venation (especially the rather distally branching CuA connected with M by M_5) to representatives of the family Protoblattinidae of the order Reculida (Aristov, in press).

The family Kortshakoliidae was erected for the genera *Kortshakolia* and *Paridelia* (Storozhenko, 1997); the genus *Vologdoptera* from the Severodvinian locality Isady, Vologda Region, Russia, was later described in this family (Aristov, 2009b). Re-examination of the holotype of *Kortshakolia ideliformis* Sharov, 1961 has shown that in this species RS begins not so distally as figured in the original description, M_5 is present, and CuA has sparse posterior branches and divides rather distally (Figs 16–18). The venation of *Kortshakolia* is typical of Permotermopsidae and especially similar to that of *Permofossilis* Aristov, 2013. *Kortshakolia* is distinguished by the rather proximally branching MP and rather distally branching CuA, which has a smaller number of branches. Based on this similarity, *Kortshakolia* is transferred here to Permotermopsidae, with which Kortshakoliidae is synonymized. *Paridelia*, the other genus of Kortshakoliidae, is placed here in Mesorthopteridae (see above). The genus *Vologdoptera*, described in Kortshakoliidae, is characterized by dense and straight anterior branches of SC, by the base of RS and first bifurcation of M situated in the middle of the wing, and by CuA abundantly branching and parallel to the anterior margin of the wing (Aristov, 2009b). This combination of characters is atypical of Eoblattida, but typical of Orthoptera. Therefore, *Vologdoptera maculosa* Aristov, 2009 is transferred here to Orthoptera incertae sedis.

Genus *Belebey* Aristov, gen. n.

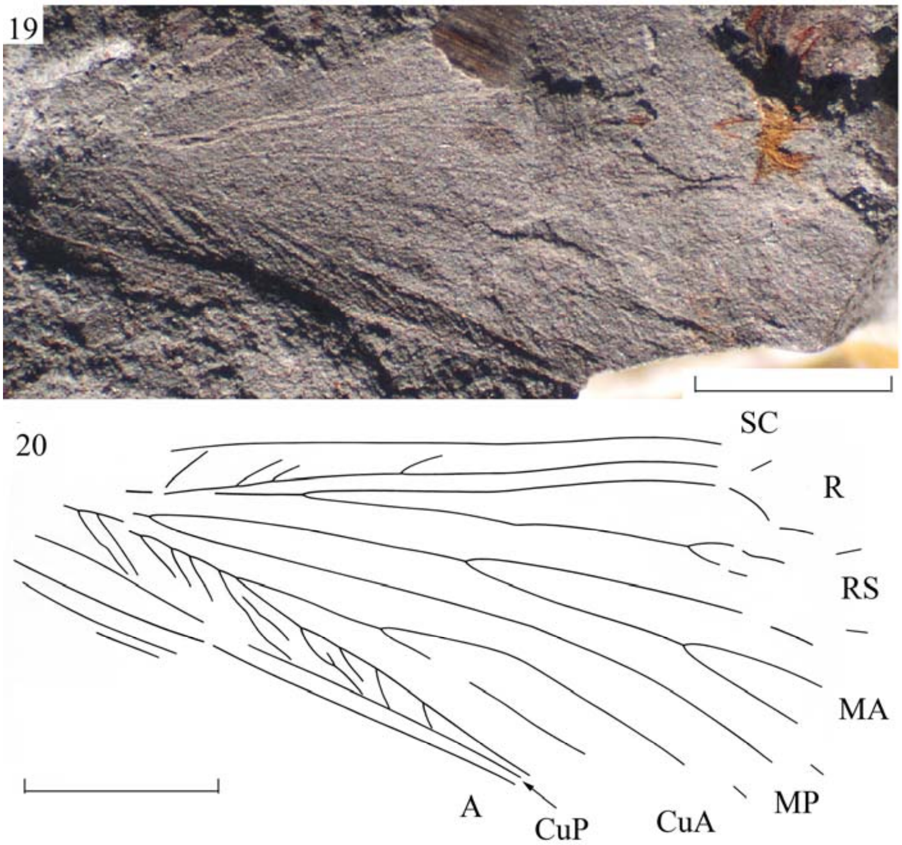
Type species: *Belebey mutilus* sp. n., here designated.

DESCRIPTION. Medium-sized insects. Anterior margin of forewing straight. Costal space at base of RS 2.5 times as wide as subcostal space. RS beginning at end of basal third of wing. MA starting branching in the middle of the wing; MP simple. CuA with dense posterior branches almost reaching posterior margin of wing, dividing distal to its basal third, three-branched. A_1 simple; A_2 branching.

DIAGNOSIS. The new genus is especially similar to *Idelina* and differs from it in MA branching in the middle of the wing, MP simple, and CuA rather proximally dividing, three-branched. In *Idelina* MA has a short bifurcation, MP divides, and CuA is five-branched, starting branching at its middle (Aristov, 2015b).

SPECIES INCLUDED. Type species only.

ETYMOLOGY. From Belebeevo Fm. Gender masculine.



19, 20. *Belebey mutilus* Aristov, gen. et sp. n., holotype PIN, No 1366/404, forewing. 19 – general appearance; 20 – reconstruction Scale bar 3 mm.

Belebey mutilus **Aristov, sp. n.**
Figs 19, 20

MATERIAL. Holotype PIN, No 3353/191, positive and negative imprints of forewing; Russia, Kirov Region, Mamlyzh District, Mamlyzh District, left bank of the Kityak River opposite Bolshoi Kityak village, Kityak locality; Middle Permian, Upper Kazanian Substage, Belebeevo Fm.; in PIN.

DESCRIPTION. SC ending in distal quarter of wing, with simple anterior branches. RS with bifurcation in distal third of wing, MA with three or more branches. A_2 with more than two branches.

MEASUREMENTS. Forewing length about 20 mm.

ETYMOLOGY. From the Latin *mutilus* (mutilated).

Family Euryptilonidae Martynov, 1940

Euryptilonidae Martynov, 1940: 15; Sharov, 1961: 161; 1962: 117; Rasnitsyn, 1980: 152; Carpenter, 1992: 119; Storozhenko, 1997a: 6; 1997b: 63; 1998: 80; 2002: 113; Aristov, 2002: 254; 2004a: 98; 2009a: 41; 2011c: 26; Aristov & Rasnitsyn, 2012: 50; 2015: 21; Aristov, 2015a: 89.

Lemmatophoridae (partim): Kukalova, 1964: 92; Storozhenko, 1991: 113; Carpenter, 1992: 106.

Lemmatophorinae (partim): Kukalova, 1964: 92; Storozhenko, 1991: 113.

Parapriscinae (partim): Kukalova, 1964: 105.

Stereopteridae Carpenter, 1950: 201 (synonimized by Storozhenko, 1997a: 6); Carpenter, 1966: 72; Sharov, 1962: 124; Rasnitsyn, 1980: 152; Carpenter, 1992: 115.

Type genus: *Euryptilon* Martynov, 1940.

DIAGNOSIS. Head hypognathous with small eyes, without ocelli, and with short antennae. Paranota wide with notch on anterior margin. Coxae large, not closely set. Meso- and metatibiae directed posteriad, tibiae and tarsus with armature; tarsus five-segmented, without arolium. SC ending on C, costal space distal to apex of SC wide. R with posterior branches (except in *Euryptilodes*). RS beginning in basal half of wing; interradial space not narrowed. Base of M fused with CuA; M starting branching near base of RS in basal half of wing. CuA without posterior branches, starting branching in its basal quarter, branching irregularly or pectinate anteriad. Clavus present; cerci shortened.

COMPOSITION. Four genera: *Euryptilon* Martynov, 1940 from Chekarda (Russia, Perm Region; Lower Permian, Kungurian Stage); *Stereopterum* Carpenter, 1950 from Elmo and Midco (United States, Kansas and Oklahoma, respectively; Lower Permian, Leonardian Stage); *Euryptilodes* Sharov, 1961 from Chekarda and Kaltan (Russia, Kemerovo Region; Middle Permian, Kazanian Stage) and *Jubala* Aristov et Rasnitsyn, 2015 from Chekarda.

NOTES. Representatives of Euryptilonidae, especially the genus *Stereopterum*, are close to representatives of the family Lemmatophoridae (order Reculida). It is very difficult to draw the line between *Stereopterum* on the one hand and the genera *Blania* Kukalová, 1964, *Maculopterum* Kukalová, 1964, *Oborella* Kukalová, 1964, *Quercopterum* Kukalová, 1964, *Sharovipterum* Kukalová, 1964, *Torrentopterum* Kukalová, 1964, and *Villopterum* Kukalová, 1964 from the Sakmarian Obora, Czech Republic, on the other hand. The above-listed genera were described in Lemmatophoridae (Kukalová, 1964) and later transferred to Euryptilonidae (Storozhenko, 1997b). In *Quercopterum* and *Sharovipterum,* the paranota of the pronotum are without notch on the anterior margin. The wing venation is oligomerized and ordered; the costal space distal to the apex of SC is narrow; CuA is divided into CuA_1 and CuA_2; the clavus is absent. On the whole, these two genera are much more similar to *Lemmatophora* Sellards, 1909 than to *Euryptilon*, and I treat them as lemmatophorids. The forms that I include in Euryptilonidae have CuA not divided into CuA_1 and CuA_2. One exception is *Stereopterum,* which has more or less developed CuA_1 and CuA_2. However, this genus is characterized by the wide costal space distal to the apex of the convex SC or by posterior branches of R and clavus, which are atypical of Lemmatophoridae. The nymphs of *Euryptilodes horridus* Sharov, 1961 (= *E. cascus* Sharov, 1961; Storozhenko, 1998) from the Middle Permian of Russia and *Triaseuryptilon acostai* (Marquat, 1991) from the Middle Triassic of Argentina (Storozhenko, 1997c) have been excluded from Euryptilonidae (Aristov *et al.,* 2006).

Family Bardapteridae G. Zalessky, 1944

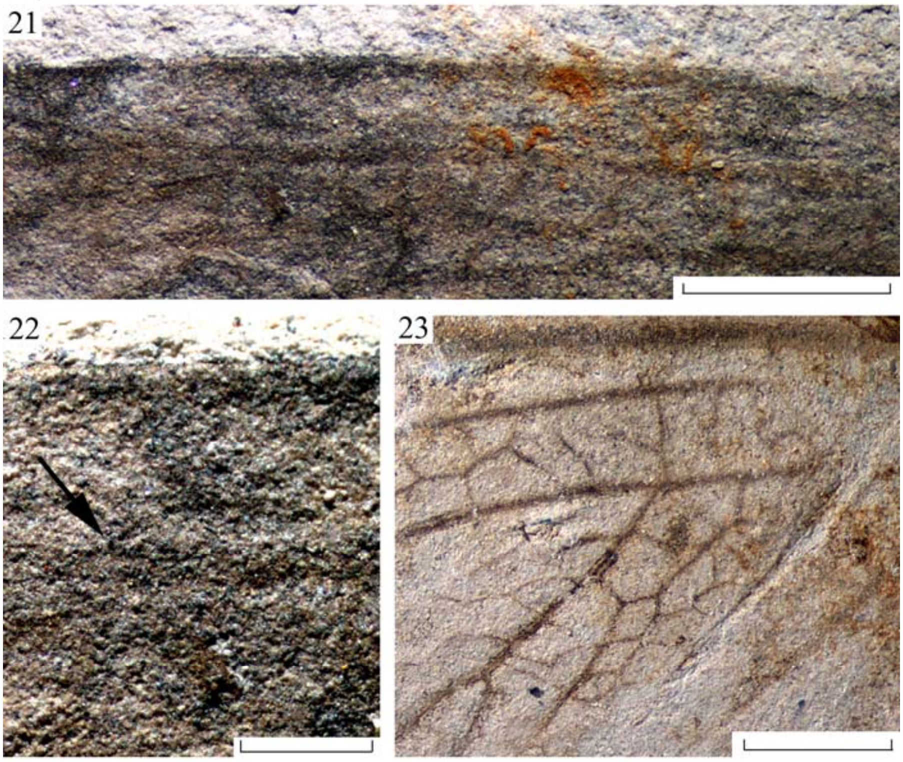
Bardapteridae G. Zalessky, 1944: 343; Rhodendorf, 1962: 53.

Type genus: *Bardapteron* G. Zalessky, 1944.

DIAGNOSIS. Forewing with SC ending on R, R without posterior branches (except in *Olgaephilus* Storozhenko, 1990). RS beginning in basal third of wing; interradial space narrowed. Base of M free; M_5 absent; M branching near base of RS in basal third of wing; MP branching near its base. CuA with posterior branches, beginning irregularly branching in its basal quarter. Clavus absent.

COMPOSITION. Four genera: *Bardapteron* G. Zalessky, 1944 from Barda (Russia, Perm Region; Lower Permian, Kungurian Stage); *Olgaephilus* Storozhenko, 1990; *Letopala* Aristov et Rasnitsyn, 2011 from Soyana (Russia, Arkhangelsk Region; Middle Permian, Kazanian Stage); and *Issadische* Aristov, 2013 from Isady (Russia, Vologda Region; Upper Permian, Severodvinian Stage).

NOTES. *Olgaephilus* Storozhenko, 1990 from Soyana was described in the family Atactophlebiidae. In *O. emendatus* Storozhenko, 1990, R has posterior branches, M_5 is absent, and M can branch distal to the base of RS. Re-examination of the type material has shown that in the forewing of this species SC ends on R, and CuA has posterior branches in the intercubital space (Figs 21–23). These characters are atypical of atactophlebiids (in which SC ends on C, M_5 is present, M branches proximal to the base of RS, and CuA has no posterior branches; see above). The genus *Bardapteron* was placed in the monotypic family Bardapteridae G. Zalessky, 1944 in the order Permodictyoptera (G. Zalessky, 1944); *Bardapteron* was later assigned to Palaeodictyoptera (Rohdendorf, 1962), Paleoptera, or Insecta incertae sedis (Carpenter, 1992; Sinichenkova, 2002). After re-description, the type species of the genus, *B. ovale* G. Zalessky, 1944, was assigned to Atactophlebiidae, based on its similarity with *Olgaephilus* (Aristov, 2004a). In this study, *Olgaephilus* is transferred to Bardapteridae. The genera *Letopala* and *Issadische* were described as eoblattids of unclear systematic position, because they are represented by incompletely preserved specimens (Aristov & Rasnitsyn, 2011; Aristov, 2013). These genera are characterized by the extremely rare combination of the absent M_5 and posterior branches of CuA. Among Eoblattida, this combination of characters is found only in *Olgaephilus*; based on this combination, which is the main distinguishing feature of Bardapteridae, the genera *Letopala* and *Issadische* are tentatively assigned to this family.



Figs 21–23. Fragments of forewing of *Olgaephilus emendatus* Storozhenko, 1990, paratype PIN, No 94-134. 19, 20 – apex of SC; 21 – base of M and CuA. Scale bar in figs 19, 21 – 3 mm, in fig. 20 – 1 mm.

Family Megakhosaridae Sharov, 1961

Megakhosaridae Sharov, 1961: 178; 1962: 132; Rasnitsyn, 1980: 154; Carpenter, 1992: 118; Storozhenko, 1993: 100; 1994: 51; 1997a: 16; 1997b: 65; 1998: 163; 2002: 279; Aristov, 2004a: 127; 2008: 4; Huang *et al*., 2008: 21; Aristov, 2009a: 40; 2009b: 19; 2010: 35; Aristov *et al*., 2011: 42; Aristov, 2013a: 52; 2013b: 763; Aristov & Rasnitsyn, 2013: 24; Storozhenko & Aristov 2014: 6; Aristov, 2015a: 90; 2015b: 1314.

Liomopteridae: Riek, 1976: 758 (partim).

Type genus: *Megakhosara* Martynov, 1937.

DIAGNOSIS. Head large, prognathous; eyes in most cases large; ocelli present. Paranota moderately wide or dilating anteriad, with rather shallow notch on anterior margin. Pterothorax with sternal suture, coxae rather small, closely set. All three pairs of legs subequal in length; meso- and metatibiae directed posteriad. Apices of tibiae without armature; tarsus five-segmented. Forewing with costal space as wide as or narrower than subcostal space; SC ending on C. RS beginning in basal third of wing; interradial space not narrowed. M_5 present, less often stem of M fused with CuA (then M diverging from CuA in one stem). M starting branching proximal to base of RS in basal quarter of wing. CuA with posterior branches, starting branching in its basal half, in most cases pectinate posteriad. Clavus absent. Ovipositor short, male genitalia symmetrical; cerci short.

COMPOSITION. 20 genera: *Megakhosara* Martynov, 1937; *Syndesmorpha* Martynov, 1937, from Kargala (Russia, Orenburg Region; Middle Permian, Urzhumian Stage); *Megakhosarella* Sharov, 1961 from Tyulkino (Russia, Perm Region; Lower Permian, Ufimian Stage), Soyana (Russia, Kemerovo Region; Middle Permian, Kazanian Stage), and Suriekova I (Russia, Kemerovo Region; Upper Permian, Severodvinian Stage); *Miolopterina* Riek, 1973; *Liomopterina* Riek, 1973 from Mooi River (South Africa, Kwazulu-Natal; Upper Permian, Wuchiapingian Stage); *Mesoblattogryllus* Storozhenko, 1990 from Madygen (Kyrgyzstan, Osh Region; Middle Triassic, Ladinian Stage); *Protoblattogryllus* Storozhenko, 1990 from Karaungir II (Kazakhstan, East Kazakhstan Region; Middle Permian, Wordian Stage), Nedubrovo, Anakit, Babii Kamen (Russia: Vologda Region, Krasnoyarsk Region, and Kemerovo Region, respectively; Upper Permian, Vyatkian Stage) and Madygen; *Megablattogryllus* Storozhenko, 1990 from Madygen; *Megakhosarodes* Storozhenko, 1993 from Karaungir I (Kazakhstan, East Kazakhstan Region; Middle Permian, Wordian Stage), Isady (Russia, Vologda Region; Upper Permian, Severodvinian Stage), Balymotikha (Russia, Vladimir Region; Upper Permian, Vyatkian Stage), Anakit, the Vosges (France, Alsace and Lorraine; Middle Triassic, Anisian Stage), and Madygen; *Megakhosarina* Storozhenko, 1993 from Kaltan (Russia, Kemerovo Region; Middle Permian, Kazanian Stage), Chepanikha (Russia, Udmurtia; Middle Permian, Urzhumian Stage), and Balymotikha; *Parakhosara* Storozhenko, 1993 from Chekarda, Vorkuta (Russia, Komi Republic; Lower Permian, Kungurian and Ufimian stages, respectively), Soyana, and Isady; *Microkhosara* Storozhenko, 1993 from Kityak (Russia, Kirov Region; Middle Permian, Kazanian Stage); *Metakhosara* Storozhenko, 1993 from Madygen; *Tshekhosara* Novokshonov, 1998; *Pectinokhosara* Aristov, 2004 from Chekarda; *Ivakhosara* Aristov, 2008 from Tyulkino (Russia, Perm Region; Lower Permian, Ufimian Stage) and Soyana; *Kargalokhosara* Aristov, 2008 from Kargala; *Madygenocephalus* Aristov, 2011 from Madygen; *Abbrevikhosara* Aristov, 2013 from Isady and *Blattokhosara* Aristov et Storozhenko, 2014 from Soyana.

NOTE. The genus *Liomopterina* was synonymized under *Liomoptoides* (Riek, 1976). However, the wing venations of the holotype of *Liomoptoides similis* Riek, 1973 (wing apex) and holotype of *Liomopterina clara* Riek, 1973 (wing base) do not overlap. It appears impossible to prove that these two fossils belong to the same species. The complete megakhosarid forewing identified as *Liomoptoides* (Dijk & Geertsema, 1999, figs. 13, 14) cannot be assigned with certainty to any of these genera. Therefore, I treat these genera as separate and the incompletely preserved *Liomoptoides* as Plecopteroidea incertae sedis.

Family Blattogryllidae Rasnitsyn, 1976

Blattogryllidae Rasnitsyn, 1976: 503; 1980a: 152; Storozhenko, 1997a: 16; 1997b: 65; 1998: 170; 2002: 280; Huang *et al.*, 2008: 21; Aristov & Zessin, 2009: 31; Aristov, 2011d: 65; Aristov *et al.*, 2011: 42; Aristov & Storozhenko, 2011: 14; Aristov, 2013a: 53; 2013b: 764; Aristov & Rasnitsyn, 2013: 24; Storozhenko & Aristov 2014: 19.

Plesioblattogryllidae Huang *et al.*, 2008: 18 (sinonimized by Storozhenko & Aristov, 2014: 19); Ren & Aristov, 2011: 273; Cui, 2012: 167.

Type genus: *Blattogryllus* Rasnitsyn, 1976.

DIAGNOSIS. Head very large, prognathous, with rather small eyes and ocelli. Paranota moderately wide, or dilating anteriad with notch on anterior margin. Pterothorax with sternal suture, coxae large, closely set. All three pairs of legs subequal in length; meso- and metatibiae directed posteriad. Apices of tibiae with armature; tarsus five-segmented with paired pulvilli on tarsomeres 1–4 and rather small arolium on tarsomere 5 (absent in *Plesioblattogryllus* Huang, Nel et Petrulevičius, 2008). Forewing with costal space at base of RS as wide as or narrower than subcostal space; SC ending on C. RS beginning in basal half of wing; interradial space narrow. Base of M fused with CuA, MA and MP diverging from CuA in separate stems. CuA with posterior branches, starting branching in its basal half (except in *Mallorcagryllus* Aristov et Zessin, 2009, *Vosgesopterum* Aristov, Grauvogel-Stamm et Marchal-Papier, 2011, *Embigryllus* Aristov, Grauvogel-Stamm et Marchal-Papier, 2011, and some *Dorniella* Bode, 1953), in most cases three-branched. Clavus absent; venation of remigium in forewing and hindwing similar; hindwing with CuA convex. Ovipositor long, male genitalia asymmetrical; cerci long.

COMPOSITION. 13 genera: *Blattogryllus* Rasnitsyn, 1976 from Karatau (Kazakhstan, South Kazakhstan Region; Upper Jurassic, Karabastau Fm.) and Sogyuty (Kyrgyzstan, Issyk Kul Region; Lower Jurassic, Jil Fm.); *Griphopteron* Handlirsch, 1939 from Dobbertin (Germany, Mecklenburg-Vorpommern; Lower Jurassic, Toarcian Stage); *Dorniella* Bode, 1953, from the Vosges (France, Alsace and Lorraine; Middle Triassic, Anisian Stage), Madygen (Kyrgyzstan, Osh Region; Middle Triassic, Ladinian Stage), Grassel and Beienrode (Germany, Lower Saxony; Lower Jurassic, Toarcian Stage); *Baharellus* Storozhenko, 1988 from Madygen and Bakhar (Mongolia, Bayankhongor Province; Middle or Upper Jurassic, Bakhar Group); *Anablattogryllus* Storozhenko, 1990 from Madygen; *Baharellinus* Storozhenko, 1992 from Isady (Russia, Vologda Region; Upper Permian, Severodvinian Stage), Babii Kamen and the Vosges; *Costatoviblatta* Storozhenko, 1992 from Madygen and Sagul (Kyrgyzstan, Osh Region; Lower Jurassic, Sogul Fm.); *Mallorcagryllus* Aristov et

Zessin, 2009 from Port de Estellencs (Spain, Mallorca; Lower Triassic, Lower Buntsandstein); *Vosgesopterum* Aristov, Grauvogel-Stamm et Marchal-Papier, 2011; *Embigryllus* Aristov, Grauvogel-Stamm et Marchal-Papier, 2011 from the Vosges; *Permoblattogryllus* Aristov, 2011 from Soyana (Russia, Arkhangelsk Region; Middle Permian, Kazanian Stage); *Plesioblattogryllus* Huang, Nel et Petrulevičius, 2008 and *Duoduo* Cui, 2012 from Daohugou (China, Inner Mongolia; Middle Jurassic, Jiulongshan Fm.).

Family Daldubidae Storozhenko, 1996

Daldubidae Storozhenko, 1996a: 18; 1997a: 4; 1997b: 65; 1998: 68; 2002: 279; Béthoux, 2008b: 224; Aristov, 2012: 253; Aristov & Rasnitsyn, 2013: 24.

Type genus: *Dalduba* Storozhenko, 1996.

DIAGNOSIS. In *Batkentak* gen. n., forewing with false costa, costal space at base of RS wider than or as wide as subcostal space, SC ending on C. RS beginning in basal half of wing; interradial space not narrowed. M_5 diverging from MP, fused with CuA markedly basal to its division into branches. M starting branching in basal third of wing, proximal to base of RS. CuA with posterior branches, starting branching at its middle, pectinate anteriad or posteriad. Clavus absent.

COMPOSITION. Three genera: *Dalduba* Storozhenko, 1996; *Vrezalduba* Storozhenko, 1996 from Chunya (Russia, Krasnoyarsk Region; Upper Carboniferous, Kasimovian Stage); and *Batkentak* gen. n. from Madygen (Kyrgyzstan, Osh Region; Middle Triassic, Ladinian or Carnian Stage).

Genus ***Batkentak*** Aristov, gen. n.

Type species: *Batkentak intactus* sp. n., here designated.

DESCRIPTION. Small insects. Anterior margin of forewing weakly concave. Precostal space narrow, “C” short. Costal space at base of RS as wide as subcostal space. R ending on anterior margin of wing, with sharp curve near apex. RS beginning in the middle of the wing, free, with branches ending on anterior margin and apex of wing. M_5 diverging from MP; MA desclerotized medially. CuA with S-shaped, simple posterior branches in intercubital space and small number of endings on posterior margin of wing. A_1 and A_2 simple. Crossveins simple. In basal third of hindwing costal space as wide as subcostal space. R and proximal branch of RS ending on anterior margin of wing. M branching basally of wing. CuA starting branching at its middle, with posterior branches in intercubital space. A_1 ending distal to middle of wing.

SPECIES INCLUDED. Type species only.

DIAGNOSIS. The new genus is especially similar to *Dalduba* and differs from it in the small size, convex anterior margin of the wing, narrow costal space, and simple S-shaped posterior branches of CuA. In *Dalduba,* the forewing length is 39–42 mm, the anterior margin of the forewing is convex, the costal space is wider than the subcostal space, and the posterior branches of CuA are lost among cells of cross-veins (Aristov, 2012).

ETYMOLOGY. From Batken Distict and the Kyrgyz "tak" (imprint). Gender masculine.

Figs 24, 25. *Batkentak intactus* Aristov, gen. et sp. n., holotype PIN, No 2785/2179, general appearance. Scale bar 1 mm.

Batkentak intactus **Aristov, sp. n.**

Figs 24–28

MATERIAL. Holotype PIN, No 2785/2179, positive and negative imprints of forewing and hindwing; Kyrgyzstan, Osh Region, Batken District, Madygen landscape unit, Madygen locality; Middle Triassic, Ladinian or Carnian Stage, Madygen Fm.; in PIN.

DESCRIPTION. Forewing with SC ending in distal third of wing. RS and MA two-branched; MP simple. CuA starting branching distal to basal third of wing, with three or four endings, ending in distal third of wing. Hindwing with six endings of RS, MA, and MP. CuA three-branched.

MEASUREMENTS. Reconstructed forewing length about 14 mm; reconstructed hindwing length about 12 mm.

ETYMOLOGY. The Latin *intactus* (intact).

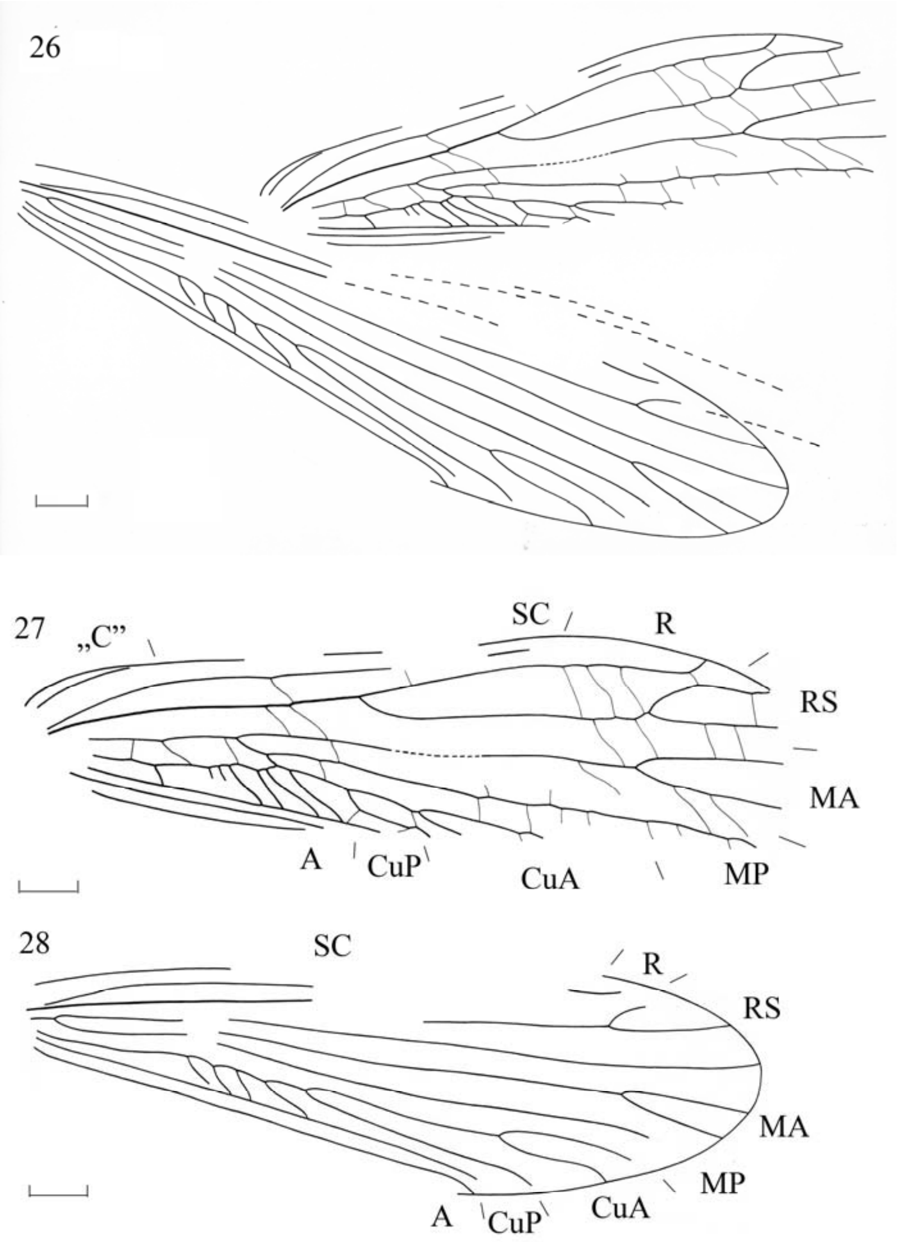
Family Idelinellidae Storozhenko, 1997

Idelinellidae Storozhenko, 1997a: 11; 1998: 116; 2002: 280; Aristov, 2004: 125; 2009a: 42; Aristov & Rasnitsyn, 2012: 50; Aristov, 2015a: 84.

Type genus: *Idelinella* Storozhenko, 1997.

DIAGNOSIS. Head hypognathous (except in *Permostriga* Novokschonov, 1999), with rather small eyes, without ocelli (except in *Permostriga*). Pronotum with very wide paranota with deep notch on anterior margin (in *Cucullistriga* Aristov et Rasnitsyn, 2012 and *Scutistriga* Aristov et Rasnitsyn, 2012, notch absent, head completely covered with paranota). Pterothorax with sternal suture, coxae set widely apart (possibly except in *Cucullistriga*), rather small. Legs shortened, all three pairs subequal in length; meso- and metatibiae directed posteriad. Forewing with costal space at base of RS wider than or as wide as subcostal space; SC ending on R (except in *Rasstriga* Aristov et Rasnitsyn, 2012). RS beginning in basal half of wing or in its middle; interradial space not narrowed. Base of M not fused with CuA (except in *Sylvastriga* Aristov, 2004); M_5 absent; M starting branching near base of RS (in *Sylvastriga* distal to base of RS) in basal half of wing. CuA without posterior branches, not dividing into CuA_1 and CuA_2 (except in *Idelinella* Storozhenko, 1997), starting irregularly branching in its basal quarter. Clavus absent; cerci short, possibly not segmented.

COMPOSITION. Seven genera: *Idelinella* Storozhenko, 1997 from Soyana (Russia, Arkhangelsk Region; Middle Permian, Kazanian Stage); *Permostriga* Novokschonov, 1999 from Soyana and Chekarda (Russia, Perm Region; Lower Permian, Kungurian Stage); *Sylvastriga* Aristov, 2004; *Strigulla* Aristov et Rasnitsyn, 2012; *Cucullistriga* Aristov et Rasnitsyn, 2012; *Scutistriga* Aristov et Rasnitsyn, 2012 from Chekarda; and *Rasstriga* Aristov et Rasnitsyn, 2012 from Mazon Creek (United States, Illinois; Upper Carboniferous, Desmoinesian Stage).



Figs 26–28. *Batkentak intactus* Aristov, gen. et sp. n., holotype PIN, No 2785/2179. 26 – fore and hindwing reconstruction; 27 – forewing reconstruction; 28 – hindwing reconstruction. Scale bar 1 mm.

Family Permopectinidae Aristov, 2005

Permopectinidae Aristov in Rasnitsyn *et al*., 2005: 411; Aristov, 2009a: 42; 2015a: 84; 2015b: 1314.

Type genus: *Permopectina* Aristov, 2005.

DIAGNOSIS. Forewing with costal space at base of RS wider than or as wide as subcostal space; SC ending on C. RS beginning in basal half of wing; interradial space not narrowed. Base of M free, M_5 absent; M starting branching proximal to base of RS in basal third of wing. CuA without posterior branches, starting branching in its basal quarter. MP and CuA pectinate posteriad, with fine branches lost among crossveins, clavus absent.

COMPOSITION. One genus: *Permopectina* Aristov, 2005 from Chekarda, Vorkuta (Russia, Komi Republic; Lower Permian, Kungurian and Ufimian stages, respectively) and Tesh (Russia, Kemerovo Region; Middle Permian, Kazanian Stage).

Family Soyanopteridae Aristov et Rasnitsyn, 2011

Soyanopteridae Aristov & Rasnitsyn, 2011: 2; 2012: 50; Aristov, 2015a: 84; Shcherbakov, 2015: 197.

Type genus: *Soyanoptera* Aristov et Rasnitsyn, 2011.

DIAGNOSIS. Head prognathous, with rather small eyes. Paranota very wide, with wide notch on anterior margin. Legs shortened, all three pairs subequal in length, coxae set widely apart. Meso- and metatibiae directed posteriad. Forewing with costal space at base of RS wider than subcostal space; SC ending on R. RS beginning in basal half of wing; interradial space narrowed; radial space strongly dilated, crossed with strong crossveins continued as branches of RS. M_5 absent; M starting branching near base of RS in basal third of wing. CuA without posterior branches, starting irregularly branching in its basal quarter (in *Poldarsia* branching distal to its middle, pectinate posteriad). Clavus absent; cerci short.

COMPOSITION. Three genera: *Soyanoptera* Aristov et Rasnitsyn, 2011 from Soyana (Lower Kazanian Substage of Arkhangelsk Region); *Stereosylva* Aristov, 2002 from Chekarda (Kungurian Stage of Perm Region); and *Poldarsia* Aristov et Rasnitsyn, 2011 from Isady (Upper Severodvinian Substage of Vologda Region).

NOTES. The structure of CuA in *Poldarsia* is typical of the order Cnemidolestida. However, because of the structure of the radial space this genus is placed in Soyanopteridae. The strongly dilated radial space crossed with strong crossveins continued as branches of RS is unique among Blattidea. The family is placed in Eoblattida because of the presence of paranota and general similarity to the family Idelinellidae.

Family Doubraviidae Aristov, fam. n.

Type genus: *Doubravia* Kukalová, 1964.

DESCRIPTION. Medium-sized insects. Head hypognathous with large eyes. Paranotal ring dilated anteriorly, without notch on anterior margin. Legs of medium length; fore and midlegs subequal in length; hind legs somewhat longer. Meso- and metatibiae directed posteriad. Forewing with costal space at base of RS wider than subcostal space; SC ending on C. RS beginning in basal third of wing; interradial space dilated. M_5 joining CuA proximal to its division into branches (in some specimens of *Koshelevka megakhosaroides* comb. n. joining CuA_1); M starting branching proximal to base of RS in basal third of wing. CuA with posterior branches in intercubital space, divided into CuA_1 and CuA_2. Clavus absent.

GENERA INCLUDED. Three genera: *Doubravia* Kukalová, 1964 from Obora (Lower Permian, Sakmarian Stage of Moravia, Czech Republic); *Koshelevka* gen. n. from Chekarda (Lower Permian, Kungurian Stage of Perm Region); and *Iva* gen. n. from Soyana (Middle Permian, Kazanian Stage of Arkhangelsk Region).

Key to genera and species of the family Doubraviidae

1 (2) Costal space in basal third of wing comparable in width with subcostal space (Figs 31-37) .... *Koshelevka megakhosaroides* (Aristov, 2004), **comb. n.**

2 (1) Costal space in basal third of wing wider than subcostal space.

3 (4) M_5 joining CuA near its first bifurcation; CuA_2 branching (Figs 29, 30) .... *Doubravia annosa* Kukalová, 1964

4 (3) M_5 joining CuA proximal to its first bifurcation; CuA_2 simple (Figs 38, 39) .... *Iva permiana* **gen. et sp. n.**

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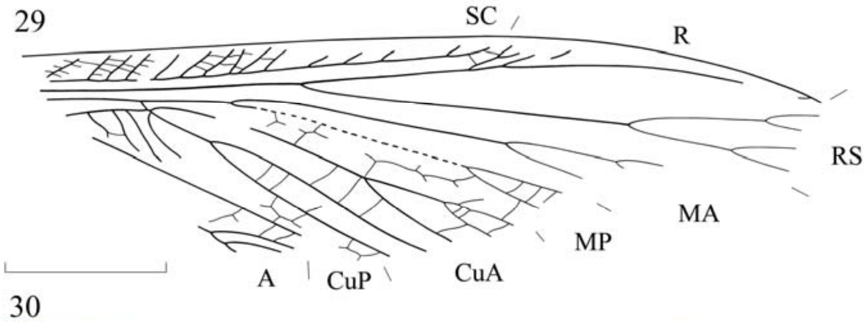


30

Figs. 29, 30. *Doubravia annosa* Kukalová, 1964, holotype DPCU, No 44/1963, forewing. 29 – reconstruction; 30 – original photograph by J. Procop (Charles University in Prague, Faculty of Science, Department of Zoology, Prague, Czech Republic). Scale bar 3 mm.

Genus *Koshelevka* Aristov, gen. n.

Type species: *Cerasopterum megakhosaroides* Aristov, 2004, here designated.

DESCRIPTION. Head large, with large eyes. Pronotum rather small, transverse. Paranotal ring square, anteriorly wider than laterally and posteriorly. Meso- and metanotum square, with indistinct scuta. Legs of medium length; fore and midlegs subequal in length; hind legs somewhat longer. Anterior margin of forewing convex. Base of costal space with costal lobe; costal space at base of RS slightly wider than subcostal space. SC with simple anterior branches, ending at beginning of distal third of wing. RS beginning at end of basal third of wing; interradial space very wide. M dividing into MA and MP immediately distal to M_5; MA and MP simple proximal to wing middle. M_5 joining CuA_1. CuA pectinate posteriad, CuA_2 simple. Intercubital space dilated basally, crossed with posterior branches of CuA. A_1 with short bifurcation. A_2 branching. Crossveins simple X and Y-shaped. Anterior margin of hindwing concave in basal half of wing, convex more distally, costal space distal to base of RS slightly wider than subcostal space. RS beginning in basal quarter of wing. CuA simple, S-shaped. Intercubital space dilated basally. Abdomen not reaching wing apices; ovipositor short.

SPECIES INCLUDED. Type species only.

ETYMOLOGY. From Koshelevka Fm. Gender feminine.

Koshelevka megakhosaroides **(Aristov, 2004), comb. n.**

Figs 31–37

Cerasopterum megakhosaroides Aristov, 2004a: 135, fig. 33c.

MATERIAL. Holotype PIN, No 4987/41, positive and negative imprints of whole insect; Russia, Perm Region, Suksun District, left bank of the Sylva River downstream of the mouth of the Chekarda River, Chekarda locality; Lower Permian, Kungurian Stage, Koshelevka Fm.; in PIN. In addition to the holotype, specimens PIN, Nos 1700/874, 3758, and 4961.

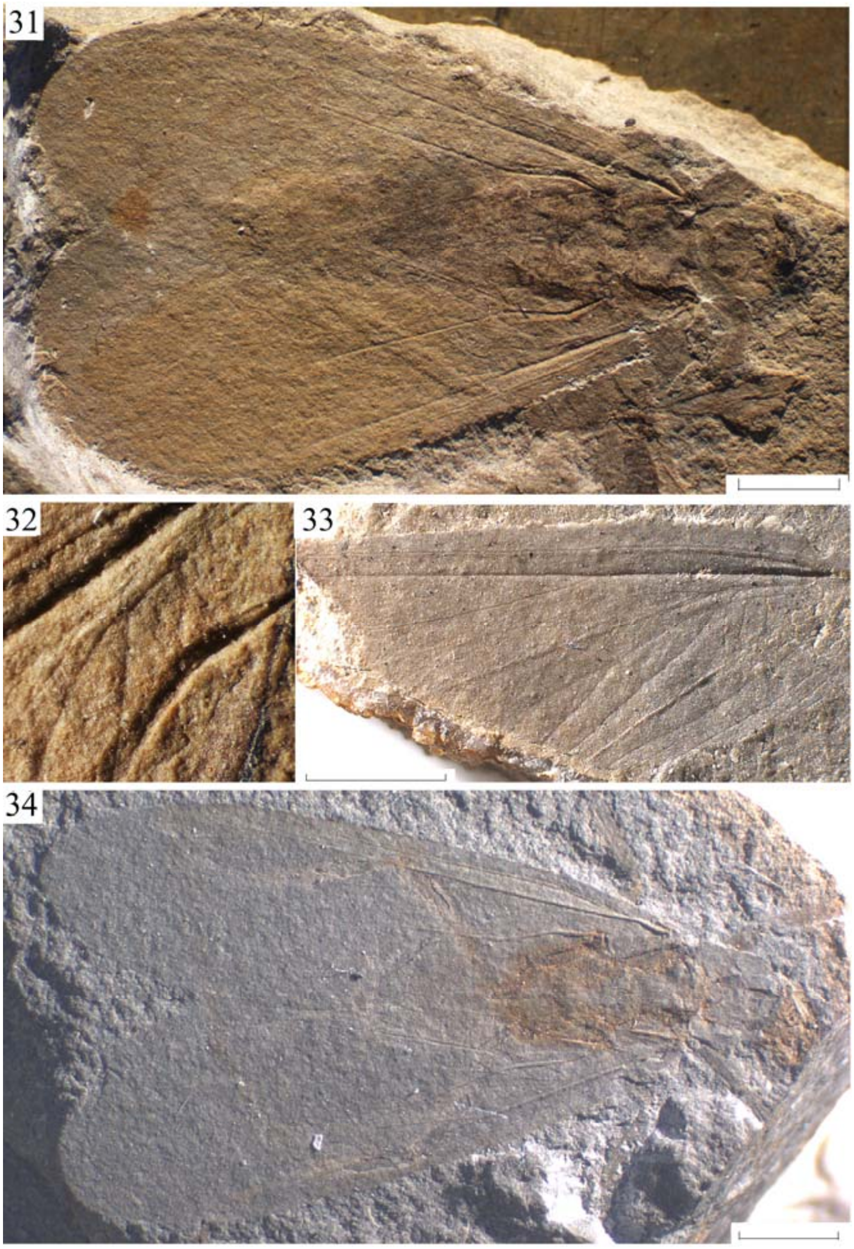
DESCRIPTION. Anterior branches of SC simple, weakly S-shaped. RS four-branched; MP starting branching distal to middle of wing; M probably with five endings. CuA_1 three or four-branched. A_2 with four or more branches.

MEASUREMENTS. Body length 18–19 mm; forewing length 20–21 mm; hindwing length about 18–19 mm.

Genus *Iva* Aristov, gen. n.

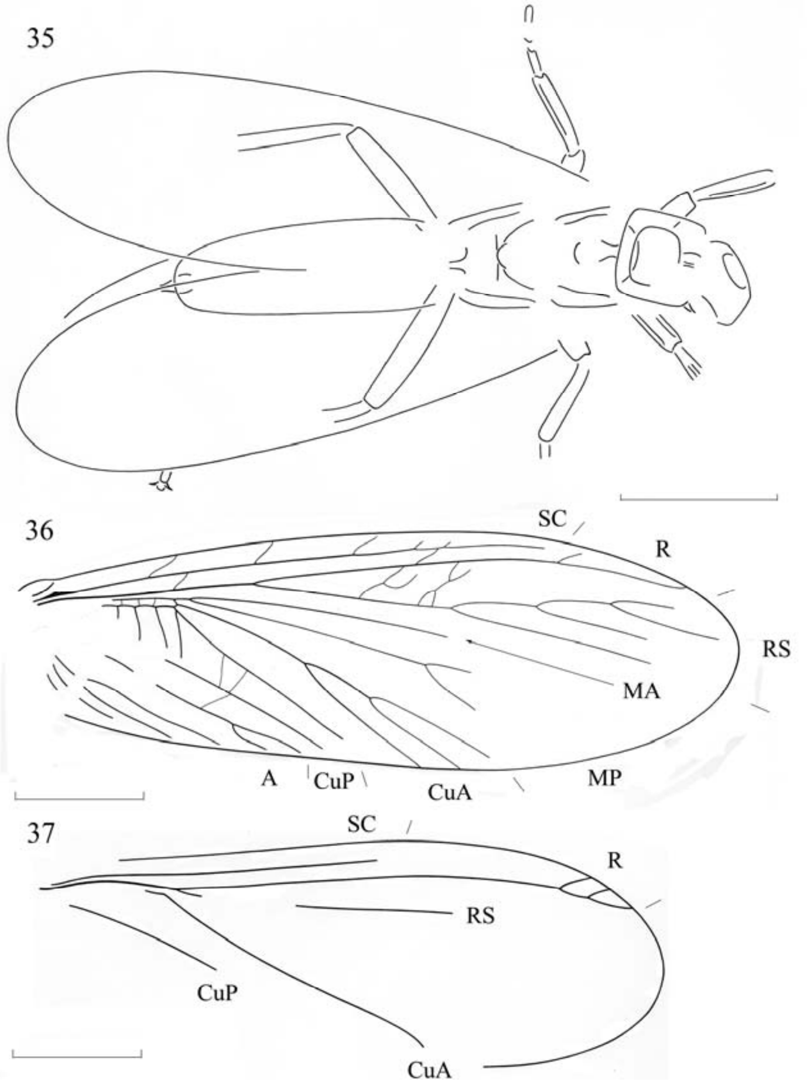
Type species: *Iva permiana* sp. n., here designated.

DESCRIPTION. Anterior margin of forewing convex. Costal space at base of RS three times as wide as subcostal space, sharply narrowing in distal third of wing. SC S-shaped, ending near apex of wing. RS beginning at end of basal third of wing; interradial space as wide as costal space. M_5 joining CuA at some distance proximal



Figs 31–34. *Koshelevka megakhosaroides* (Aristov, 2004). 31 – specimen PIN, No 1700/4961, general appearance; 32 – the same, part of forewing; 33 – specimen PIN, No 1700/3752, forewing; 34 – specimen PIN, No 1700/4031, general appearance. Scale bar 3 mm.

to its first bifurcation. M_5 and first bifurcation of M not closely set. M dividing into branches level with first bifurcation of CuA. CuA starting branching in its basal quarter; CuA_1 branching at posterior wing margin; CuA_2 simple, without posterior branches. Intercubital space sharply narrowing towards posterior margin of wing. Anal area rather small. Crossveins mostly simple.



Figs 35–37. *Koshelevka megakhosaroides* (Aristov, 2004). 35 – reconstruction of general appearance based on holotype PIN, No 4987/41 and specimen PIN, No 1700/4031; 36 – reconstruction of forewing based on holotype and specimens PIN, No 1700/874, PIN, No 3753 and PIN, No 4961; 37 – hindwing, specimen PIN, No 1700/874. Scale bar in fig. 35 – 5 mm, in figs 36, 37 – 3 mm.

SPECIES INCLUDED. Type species only.

ETYMOLOGY. From Iva-Gora beds. Gender feminine.

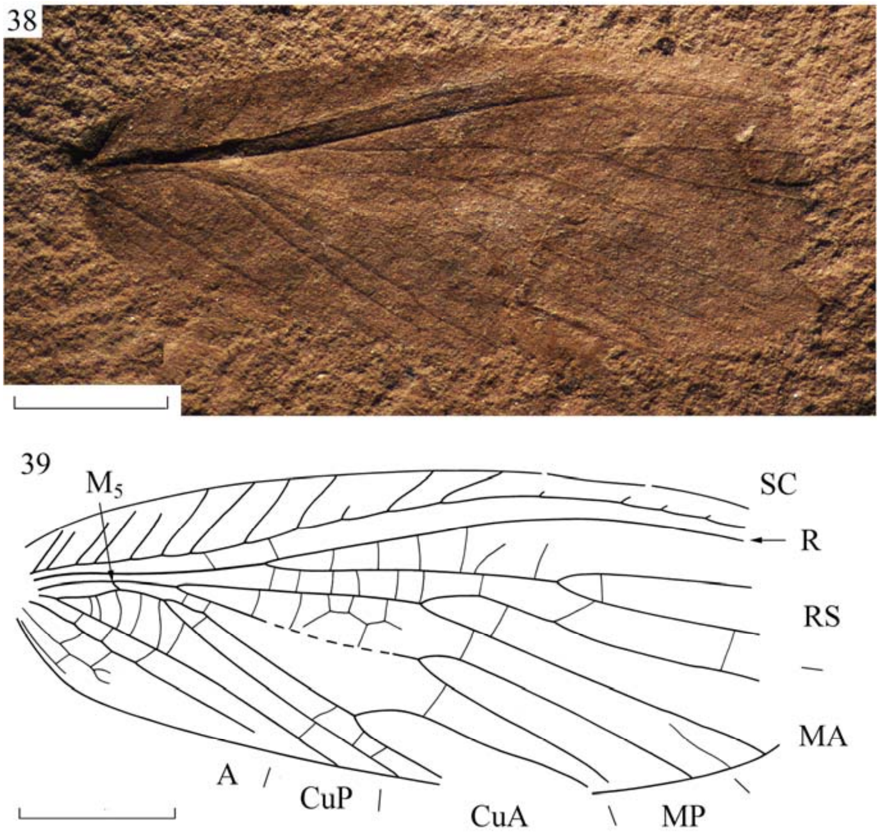
Iva permiana Aristov, sp. n.

Figs 38–39

MATERIAL. Holotype PIN, No 3353/191, negative imprint of forewing; Russia, Arkhangelsk Region, Mezen District, right bank of the Soyana River 56–60 km from its mouth, Soyana locality; Middle Permian, Lower Kazanian Substage, Iva-Gora beds; in PIN.

DESCRIPTION. SC with simple anterior branches. RS dividing into two branches in distal third of wing. MA, MP and CuA_1 with two branches each. Crossveins simple and forming double row of cells in intermedial space. A_1 simple; A_2 three-branched.

MEASUREMENTS. Forewing length about 16 mm.



Figs 38, 39. *Iva permiana* Aristov, gen. et sp. n., holotype PIN, No 3353/191, forewing. Scale bar 3 mm.

Family Grylloblattidae Walker, 1914

Grylloblattidae Walker, 1914: 93 (for full bibliography see: Storozhenko, 1998 and Wipfler *et al*., 2014).

DIAGNOSIS. Head very large, prognathous, eyes small or absent; ocelli absent. Paranota shape as narrow band along posterior margin of pronotum. Pterothorax with sternal suture; coxae large, not closely set. Meso- and metatibiae directed posteriad. Apices of tibiae with armature; tarsus five-segmented with paired pulvilli on tarsomeres 1–4 and unpaired pulvillus on tarsomere 5, without arolium. Wings reduced. Ovipositor long, male genitalia asymmetrical; cerci long.

COMPOSITION. Five extant genera: *Grylloblatta* Walker, 1914 from the United States and Canada; *Galoisiana* Caudell, 1924 from China, North and South Korea, Japan, and Russia; *Grylloblattina* Bey-Bienko, 1951 from of Russia; *Grylloblattella* Storozhenko, 1988 from Russia and China; and *Namkungia* Storozhenko et Park, 2002 from South Korea.

DISCUSSION

The structure of the body is known to date only in a small number of Carboniferous Eoblattida. They are characterized by the prognathous head and ring of paranota, with rare exceptions covering the head from above. Such paranota (in contrast to two-lobed paranota found in most Dictyoneuridea) serve to protect the wings during movement in substrates with large burrows (macrolitter or under bark). Development of the clavus in forewings is also an adaptation to living in the litter. The clavus is the anal area, in most cases more or less lanceolate, separated by a deep fold along which CuP runs. Such structure facilitates the deformation of the strengthened wings when the insect crawls into tight crevices (Gorochov, 2004) and fixation of the wings when they are folded. Another adaptation to living in the litter is the development of characteristic spines, the spurs, on apices of the tibiae. Such spurs are typical of Eoblattidae and Euryptilonidae. At the same time, the paranota in Eoblattida do not cover the head completely (as they do in Blattida), providing for sufficient field of vision and giving evidence of the relatively open mode of life of eoblattids. In addition, the legs of Carboniferous eoblattids are clearly phytophilous. The legs can be very long (in Cacurgidae; Fig. 3), and the tibiae of the mid- and hind legs in imprints are directed anteriad. This position is typical of prehensile legs, which allow phytophilous insects to move by pulling up, rather than by pushing against the substrate, as herpetobionts do. Originally, Eoblattids were probably phytophilous (thamnobiont), capable of taking shelter from danger in the litter or under bark, a mode of life more typical of many recent orthopterans (Gorochov, 1995). In the Permian, some eoblattids lost their association with plants. Although the legs of Ideliidae, Mesorthopteridae, and Blattogryllidae and not prehensile, the structure of their tarsi (the presence of a large arolium and pulvilli) gives evidence that they visited plants. Other eoblattids (Euryptilonidae, Idelinellidae, Soyanopteridae, and Grylloblattidae) became specialized stratobionts, like Blattida, but to a smaller degree. These eoblattids are characterized by enlarged paranota covering the head from the sides (but nevertheless leaving it open from above because of a notch in the anterior margin of the paranotal ring), or, by contrast, by strongly reduced paranota and wings, as in recent forms. In Grylloblattidae, paranota have been preserved as a band along the posterior margin of the pronotum. The legs in these forms became shorter (Idelinellidae, Soyanopteridae), and spurs appeared on the apices of the tibiae (Euryptilonidae, Grylloblattidae). Eoblattida were probably originally phytophagous, feeding on sporangia, possibly in combination with saprophagy. Palynophagy (probably facultative) remained typical of the Permian Ideliidae. The guts of many specimens found in the Kungurian Chekarda locality in the Perm Region are filled with pollen (Rasnitsyn & Krasilov, 1996). Stratobiont forms shifted to saprophagy; some open-living forms (such as Megakhosaridae and Blattogryllidae), judging by the structure of their mouthparts, were nonspecialized predators. Their descendants, the extant Grylloblattidae, are predators feeding on small arthropods (Storozhenko, 1998). Thus, eoblattids were originally facultative phytophiles similar in the mode of life to the predactous cnemidolestids, but different from them in feeding type (palynophagy and possibly saprophagy). They differed from the other Carboniferous Gryllones (Blattida, Reculida, and Mesotitanida) in phytophily and from primitive Orthoptera in palynophagy (palynosaprophagy). The mode of life reconstructed for primitive orthopterans is that of weakly specialized phytophilous predators capable of taking shelter from danger in the litter (Gorochov, 1995).

It is believed that the most primitive pterygotes are Namurian and Westphalian representatives of the order Paoliida (*sensu* Rasnitsyn, 2002). They were large phytophilous insects feeding on contents of sporangia. The head in Paoliida was mobile (because of the absence of paranota on the pronotum), with very long antennae. The legs were very long; the mid- and hind legs were prehensile, with the tibiae in imprints directed anteriad; the tarsi were long, with a large arolium and possibly pulvilli on tarsomeres 1–4 (Fig. 40). This combination of characters is an adaptation to living on plants. The wings are folded roof-shaped and have primitive venation; the forewings have clavus; the anal area of the hindwings is not enlarged and not bent underneath. Paoliids were probably rather immotile specialized phytobionts capable of taking shelter from danger in substrates with large burrows (macrolitter or under bark). This ability is indicated by the presence of the clavus (see above). The base of the costal space is known only in a few specimens of Paoliidae (Procop *et al.,* 2014). These specimens have no modifications of this part of the wing that could serve, among other things, as adaptations to moving in crevices (see below). This facultative phytophilous mode of life, with the ability to take shelter, was also typical of decendants of Paoliida, primitive Eoblattida (see above) and Cnemidolestida. The latter had prehensile legs with arolium and pulvilli on tarsomeres, adapted to living on plants, modified base of the costal space, and the clavus, i.e., adaptations to moving in crevices (Aristov, 2014a). The appearance of the precostal space (a special area at the base of the costal space separated by a fold or the false costa) is associated with protection of wings during movement in the litter if the paranota are absent or poorly developed. In the course of adaptation to the stratobiont mode of life, the convex base of the costal space becomes either reduced or bent downward. This bend is an additional stiffener that can be strengthened further by an extra convex vein, the false costa (“C”, or ScA). This structure of the precostal space is typical mainly of the superorder Gryllidea. In some other Gryllones, “C” is absent, and a dilated area at the base of the costal space is separated from the rest of the space by a fold (rather than a vein), often situated in front of the curved and thickened base of SC. I propose to term this structure the costal lobe. It is typical of Cnemidolestida, Reculida, some primitive Blattida, and several representatives of Eoblattida.

40

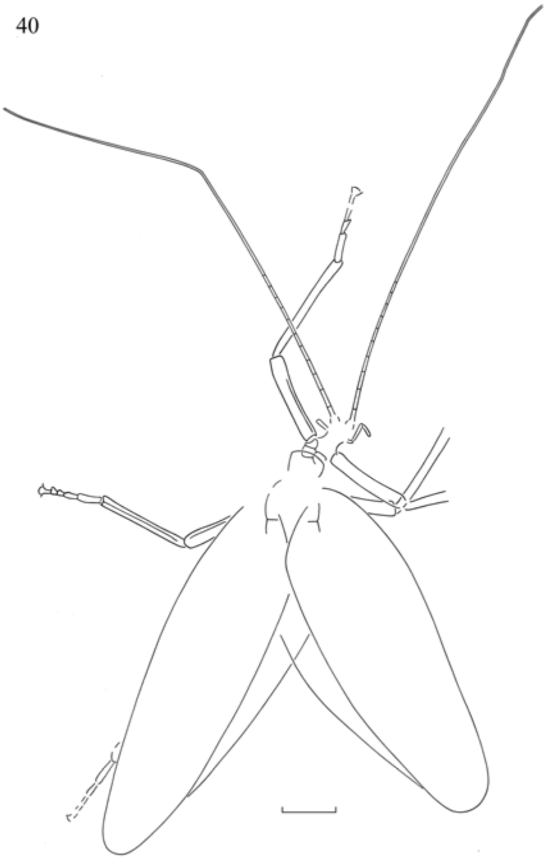


Fig. 40. General appearance of *Kemperala hagenensis* Brauckmann, 1984, original drawing based on photograph (Rasnitsyn, 2002: fig. 75). Scale bar 10 mm.

Thus, the original mode of life of pterygotes was phytophyly in combination with the ability to take shelter in substrates with large burrows. The venation of primitive Carboniferous insects is very similar. The forewings are similar in representatives of Paoliida, in *Kochopteron* (Eoblattida), and in *Heterologellus* (Dictyoneuridea). They differ in SC joining C in *Kochopteron,* in the presence of blind branches in the interradial and medial spaces in Paoliidae, and in other not very important characters. The primitive forewings of eoblattids of the family Eoblattidae and cnemidolestids of the family Ctenoptilidae are also similar and differ mainly in the presence of “C” in the latter. Another example is the similarity of forewings in hypoperlids of the family Ischnoneuridae and cnemidolestids of the family Cnemidolestidae (Rasnitsyn & Aristov, 2013; Aristov, 2014a). In the early Upper Carboniferous (Pennsylvanian), specialization of the body evolved more rapidly than specialization of the wing venation (i.e., heterobathmy took place). This phenomenon may be associated with the rather small role played by flight in primitive insects. Although the system of fossil insects is based mostly on wing venation, in this case the general structure of the body may be of decisive importance for the delimitation of orders. The reliable boundary between Paoliida and Gryllones was probably marked by the emergence of a complex of characters associated with increasing role of shelters in the life of insects. This complex of synapomorphies of the infraclass Gyllones includes the presence of paranota (or their functional counterparts, the precostal space or costal lobe), compact (flat) folding of the wings, and development of the clavus and of the anal area of the hindwing bent underneath, which evolved as a result of strengthening of the forewing and transfer of its aerodynamic functions to the hindwing. Only the clavus of all above-listed characters is typical of paoliids. Primitive Eoblattidae (Eoblattida) and Ctenoptilidae (Cnemidolestida) have a complete set of these characters. However, in the primitive eoblattids of the family Cacurgidae, only the paranota and clavus are reliably known to be present. Judging by imprints, the wings of these eoblattids (*Cacurgus* Handlirsch, 1911: Béthoux, 2006; *Kochopteron* Brauckmann, 1984: Ilger & Brauckmann, 2008) could fold in a similar manner to those of Paoliidae; the structure of the anal areas of their hindwings is unknown. Therefore, I provisionally delimit Paoliida by the absence of paranota in combination with the unmodified base of the costal space of the forewing and anal area of the hindwing.

The presence of the above-described complex of synapomorphies in both Eoblattida and Cnemidolestida suggests that they had a common ancestor. It was believed that eoblattids were ancestral to the entire infraclass Gryllones (Rasnitsyn, 2002; Gorochov, 2004). Reconstruction of the ancestor of all Gryllones as a stratobiont (Sharov, 1965; Gorochov, 2004) implies that phytophyly was secondary in eoblattids and cnemidolestids and that paranota in cnemidolestids disappeared. In my opinion, this unwarrantedly complicates the scenario of the evolution of this group. Both phytophyly and absence of paranota in cnemidolestids are probably primary, and thus Cnemidolestida could not be descendants of Eoblattida. The common ancestor of these two orders was a facultative phytophile and had prehensile legs and pronotum without paranota. The forewing of these insects had a clavus, and the anal area of the hindwing was bent underneath at rest. Externally this ancestor was probably more similar to Cnemidolestida. The divergence of Eoblattida and Cnemidolestida was associated with the shift to predation in Cnemidolestida and with the preserved palynophagy or shift to saprophagy and living in the litter in Eoblattida.

The order Eoblattida was placed in the superorder Blattidea (Rasnitsyn, 1980; Storozhenko, 1997b) or treated as incertae superordinis (Rasnitsyn, 2002). It was subsequently placed in the superorder Perlidea (Aristov & Rasnitsyn, 2009), based on the inclusion of the family Spanioderidae in Eoblattida; however, this family was later transferred to the order Cnemidolestida (Aristov, 2014a), which has placed in Perlidea. At the same time, the order Eoblattida remains strongly associated with Blattidea, essentially as the basal group of this suborder, ancestral, on the one hand, to the order Blattida, from which Mantida and Termitida later descended (Rasnitsyn, 2002), and on the other hand, to the order Reculida.

Blattida are characterized by their hypognathous head and pronotum with a wide ring of paranota, which cover most of the head or the entire head. Their pterothorax has no sternal suture; the fore legs are the shortest pair of legs; the hind legs are the longest. The coxae are large with bases set widely apart; the tibiae have armature; the tarsus is five-segmented, without pulvilli, with arolium, and with claws. The forewing is rigid, with polymerized venation. Paleozoic Blattida has the following combination of characters. The wing is strongly decostalized; the precostal space or its functional counterparts (with rare exceptions) are absent; SC is short and ends on C. R has very long anterior branches; RS begins in the basal half of the wing; R and RS are poorly differentiated. M_5 is absent; M starts branching in the middle of the wing, distal to the base of RS. CuA has no posterior branches in the intercubital space and starts branching near its base, forming a regular posterior comb of branches; this comb reached the posterior margin of the wing at an angle of about 45°. CuP is simple, arcuate, situated in a deep fold, which separates the lanceolate clavus. The ovipositor is long; the male genitalia are symmetrical; the cerci are short, segmented.

Some of the Upper Carboniferous genera of the most primitive family Archimylacridae deviate from this diagnosis. These forms preserved some characters found in Eoblattida. *Miroblatta costalis* Laurentaux-Viera et Laurentaux, 1987 from Rieu-du-Coeur (Westphalian Stage A of Belgium) had a notch on the anterior margin of the paranota (Béthoux *et al.,* 2011). SC ending on R far distal to the middle of the wing is known in *M. costalis* and *Archimylacris johnsoni* (Woodward, 1887) from Coseley (Westphalian Stage B–C of the United Kingdom). It has to be noted that this character is unstable, and in one wing SC can join C, while in the other wing of the same specimen it can join R (Béthoux *et al.,* 2011; Bolton, 1921; Schneider, 1983). *M. costalis* preserved a strong individualized R bearing only weak anterior branches. The blattid of unclear position *Qilianiblatta namurensis* Zhang *et al.,* 2012 from Xiaheyan (Namurian Stage B–C of China) has M_5 present and CuA with posterior branches in the intercubital space (Wei *et al.,* 2013). The same characters are known in some other Blattida (Béthoux, 2008b; Béthoux *et al.,* 2011). However, all above-listed primitive characters are never found together in the same fossils. The hypothetical ancestor of Blattida had all these characters together and was similar to the family Eoblattidae. Primitive Blattida were more similar in the structure of CuA to Paoliida than to Eoblattida. In *Zdenekia* Kukalová, 1958 (Paoliidae), CuA is partly pectinate posteriad and reaches the posterior margin of the wing at an angle of about 45° (Béthoux & Schneider, 2010). The most primitive Blattida probably evolved in the Namurian from a common ancestor with Eoblattidae; it is possible that this ancestor differed from Eoblattida only in CuA pectinate posteriad and according to its combination of characters belonged to that order. It probably had the head not covered with the paranota, SC long and ending on R, M_5 joining the stem of CuA, which was "paoliid," i.e., pectinate posteriad and having posterior branches in the intercubital space, and clavus present. This common ancestor was saprophagous and probably was a facultative stratobiont that had not entirely lost its association with plants. Blattida later took the specialization route of typical stratobionts and as early as in the Namurian acquired the complex of adaptations characteristic of this mode of life (see above).

The most primitive Reculida are Namurian representatives of the family Sinonamuropteridae (Cui *et al.,* 2011; Cui & Ren, 2013). This family is characterized by SC joining C or R (this character is subject to individual variation), M_5 present, and clavus more or less developed (only the base of CuP is distinctly concave). At the same time, Sinonamuropteridae already have the division of CuA into CuA_1 and CuA_2 with M_5, joining CuA basal to its division into branches; this division is very typical of Reculida. In the other reculids, SC always joins C, M_5 is lost (with rare exceptions), and the clavus is absent. Sinonamuropteridae could be descended from eoblattids similar to Protophasmatida, as a result of reduction in size and loss of some veins. These changes were accompanied by shifting of the first bifurcation of M posteriad, to the base of RS, and by the appearance of the division of CuA into CuA_1 and CuA_2 (Aristov, in preparation).

Thus, the order Eoblattida occupies a key position in the history of the infraclass Gryllones and represents (together with Cnemidolestida) the earliest descendants of Paoliida and ancestors of all other orders of Blattidea. Similarly, their sister group Cnemidolestida were ancestors of all Gryllidea and Perlidea (Aristov, 2014a).

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